SEASONAL AND ONTOGENETIC CHANGES IN

MEIOFAUNA IN THE DIETS OF

POSTMETAMORPHIC FLATFISH

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A

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Thesis Abstract

The diets of intertidal postmetamorphic (9.0-97.0 mm SL) rock sole, Lepidopsetta bilineata (Ayres 1855), starry flounder, Platichthys stellatus (Pallas 1811), and yellowfin sole, Limanda aspera Pallas 1811, were investigated over a one year period in Auke Bay, Alaska. Rock sole were collected earliest, followed by starry flounder, and yellowfin sole. Harpacticoid copepods were the primary prey of small (<20.0 mm standard length) fish of all species. Harpacticoids were also numerically important in the diets of medium (20.0-34.5 mm SL) fish, but relatively unimportant in the diets of large (>35 mm SL) fish.

Meiofauna was collected concurrently with fish samples. Settlement of flatfish did not occur when the density of harpacticoids was highest. Highest densities of total harpacticoids occurred during May in both 1987 ($2.6 \times 10^6 \pm 2.5 \times 10^5$) and 1988 ($1.4 \times 10^6 \pm 3.2 \times 10^4$). Other meiofaunal taxa did not have the same seasonal changes in density. Some minor taxa were only present seasonally.

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The body of this thesis is comprised of two manuscripts prepared for submittal to Marine Ecology Progress Series and the Journal of Fish Biology. While I was responsible for the field work, data collection and analysis, and manuscript preparation, the contributions by Dr. Thomas Shirley were substantial. I am honored to be able to list him as co-author of these publications.

CHAPTER I.

SEASONAL VARIATION OF INTERTIDAL MEIOFAUNA IN AUKE BAY, ALASKA

Introduction

Meiofauna provide an important pathway for conveying primary production to higher trophic levels. Harpacticoid copepods, commonly the second most abundant meiofaunal group in intertidal muds (Coull and Bell 1979), are especially important to the diets of many juvenile fish and crustaceans (see Gee, 1989 for review). Harpacticoids are the primary prey for some species of postmetamorphic flatfish (Hogue and Carey 1982; Hicks 1984; Morais and Bodiou 1984; Sturdevant 1987; McGregor chapter 2). Pink salmon (Oncorhynchus gorbuscha) and chum salmon (O. keta) fry diets are comprised of more than 80% harpacticoids in some areas (Kaczynski et al. 1973; Landingham 1982). Red king crab (Paralithodes camtschatica; Feder et al. 1980; Shirley et al. 1987), brown shrimp (Crangon) and shore crabs (Carcinus maenas; Gee 1987) diets also commonly contain harpacticoids. There has been little study in Alaska on the meiofauna that is an important food resource in the early life histories of these species and others (Jewett and Feder 1977; Feder et al. 1980; Landingham 1982; Cordell 1986; Sturdevant 1987; Fleeger et al., 1989; Fleeger and Shirley in press a,b; Shirley and Fleeger in press).

The subarctic is a highly seasonal environment where springtime blooms of phytoplankton contribute a large portion of the total annual primary production (Laws et al.

1988). Reproduction of zooplankton and fish is generally synchronized with the greater nutrition available during the bloom (Haldorson et al. in press). For example, the outmigration of pink and chum salmon fry to seawater is synchronized to take advantage of the pulse in zooplankton productivity (Murphy et al. 1988; Holtby et al. 1989). Prior to feeding on pelagic zooplankton, fry are dependant on nearshore benthic and epibenthic meiofauna, particularly on harpacticoid copepods (Feller and Kaczynski 1975; Sibert et al. 1977; Sibert 1979). Survival of salmon fry is undoubtedly related to meiofaunal abundance, especially harpacticoids.

The time of year when maximum densities of harpacticoids occur in southeastern Alaska is not known. Maximum densities of harpacticoids occurred in July - September in Valdez, Alaska at both sandy and muddy intertidal sites (Feder and Paul 1980). Highest annual numbers have been reported during similar times in Scotland (McIntyre and Murison 1973), but in an intertidal area in Narragansett Bay, Rhode Island, harpacticoids were most abundant in May and June and lowest in late summer and fall (Rudnick et al. 1985). Seasonal abundance peaks may be related to a variety of factors, such as temperature, food availability, species composition, and predation (Hicks and Coull 1983; Hicks 1984).

Meiofauna typically exhibit more interannual variability than seasonal variability (Coull 1985). While a long-term data set is necessary to determine interannual fluctuations in populations, a two-year monitoring period is thought to be sufficient to determine seasonality patterns (Coull and Dudley 1985). I examined seasonal trends in abundance and composition of the meiofauna at an intertidal site in Auke Bay, Alaska over a 16-month period. In a related study I examined the diets of juvenile flatfish at the same site to determine to what extent they were feeding on meiofauna, especially harpacticoid copepods (McGregor chapter 2).

Methods and Materials

Meiofauna samples were collected from an intertidal area in Auke Bay, Alaska (58° 22′ N, 134° 40′ W; Figure 1). Auke Bay is located approximately 20 km north of Juneau in southeastern Alaska. The bay is approximately 16 km ^{2} in area, 70% of which is less than 60 m in depth with a clayey-silt substrate of low sand content. A seasonal influx of glacial sediment is deposited in the bay from the Mendenhall River, which flows into adjoining Fritz Cove. Auke Bay has semi-diurnal tides with amplitudes of 3 - 7 m (Shirley in press). The hydrography and fauna of Auke Bay was reviewed in greater detail by Shirley and Coyle (1986).

The study area is located within a cove on the east side of Auke Bay and consists of a protected mudflat approximately 60 m wide with a clayey-silt substrate (Sturdevant 1987; McGregor chapter 2). Sampling was conducted on spring lower low tides along a transect parallel with the water line, located at the 0 m tidal level.

Temperature and salinity were measured synoptically with meiofauna collections. Water temperature was measured seaward of the transect in water approximately 0.5 m in depth. The temperature was recorded from immediately under the surface. Water was collected from the same location and salinity was measured with a refractometer.

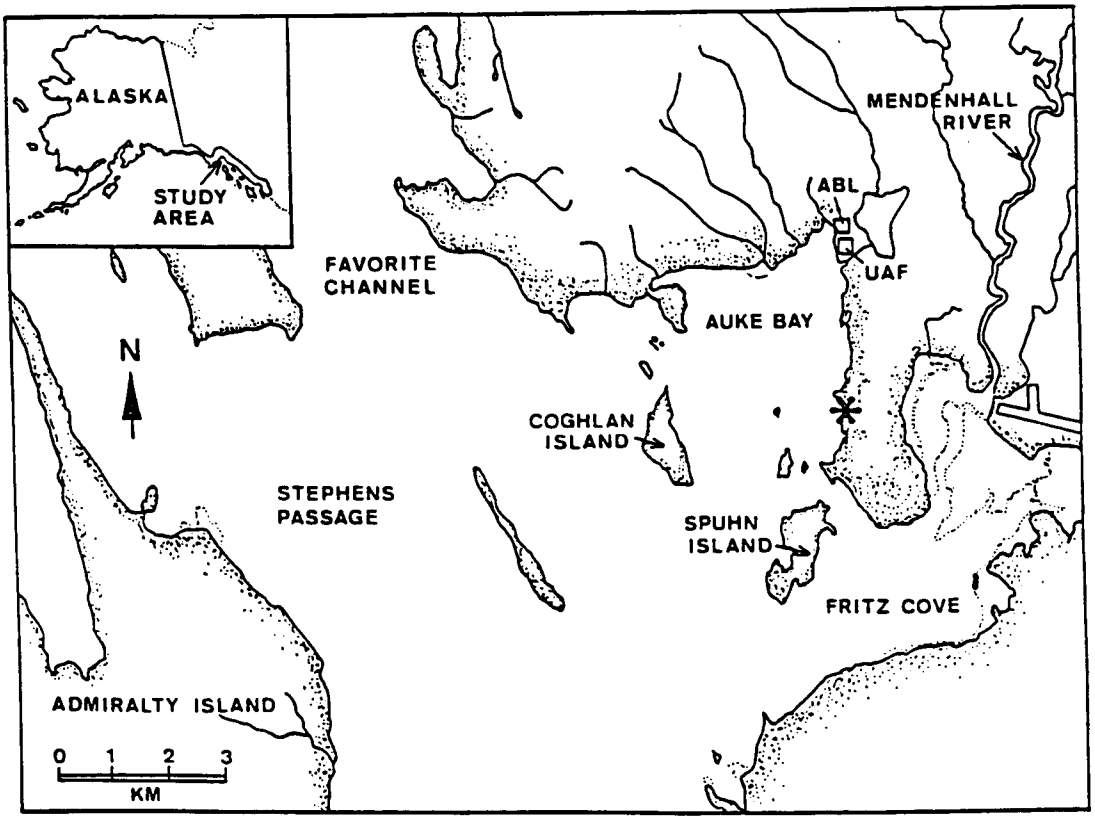

Figure 1. Study area in Auke Bay, Alaska. Asterisk marks collection site.

Locations of meiofauna collections along the transect were selected with a random number table. Samples were collected twice monthly from March through September, 1987, monthly throughout the winter, and again bi-monthly from March through June 1988. Four cores per sample date were collected using a piston corer made from a hand held 50 cc syringe. The upper 5 cm of sediment and the overlying water from each core were retained. In muddy sediments meiofauna are often restricted to the upper few cm of oxidized sediments (Coull and Bell 1979). At the lab, cores were individually processed by sieving with seawater. Organisms passing through a 0.500 mm mesh sieve but retained upon a 0.063 mm mesh sieve were extracted alive with sucrose centrifugation (Fleeger 1979). This technique was estimated to have a greater than 95% extraction efficiency with subtidal meiofauna samples from Auke Bay (Fleeger et al. 1989; Shirley in press).

All meiofaunal organisms were preserved in a 5% buffered formalin solution, stained with rose bengal, and identified to major taxon with a stereomicroscope. Nematodes, harpacticoid copepods, and copepod nauplii were very abundant in samples and were subsampled using a technique employing a triply - balanced square design (Sherman et al. 1984).

Mean densities of meiofaunal organisms were compared

among sample dates using nonparametric ANOVA (Kruskal Wallis). When significant differences were indicated, pairwise comparisons (Mann-Whitney U) were used to detect differences in densities. Few mean values for individual sample dates were significantly ($p<0.01$) different from the immediately preceding or following dates. Groups of sample dates that appeared to be similar (visually) were combined to increase sample size, and these groups were tested for statistical differences (Kruskal Wallis; Appendix A). Tests of significance mentioned hereafter generally refer to these grouped values, and not to comparisons of individual sample dates. Mean values are presented ± one standard error.

Results

Physical Parameters

Water temperatures at the study site varied seasonally, with an annual mean of 8.2°C ± 0.9. A high value of 15° C was recorded on 10 August, 1987 and a low of 3.6°C was recorded on 20 March, 1988 (Figure 2). Summer water temperatures were generally between 11 - 12°C and winter temperatures between 4 - 5° C. Intertidal temperatures at the study site were similar to surface temperatures within Auke Bay from March through June of 1987 and 1988 (Ziemann et al. 1988; Ziemann et al. 1989). The intertidal water may have been subject to more rapid variations due to daily warming and cooling from tidal water movements over warmed sediment in summer, and from snow and ice cover in winter.

Salinity also varied seasonally, with an annual mean of 23.1 °/oo ± 1.5. Highest values occurred during the winter and early spring, when freshwater runoff into Auke Bay is typically lowest. Values above 30°/oo occurred in January through April, 1988. Low salinities (16 - 18°/oo) occurred during June and July in both years and in August of 1987, corresponding to periods of warm weather and increased runoff (Figure 2). Salinity values were similar to those recorded for Auke Bay surface waters during March - June, 1987 and 1988 (Ziemann et al. 1988; Ziemann et al. 1989).

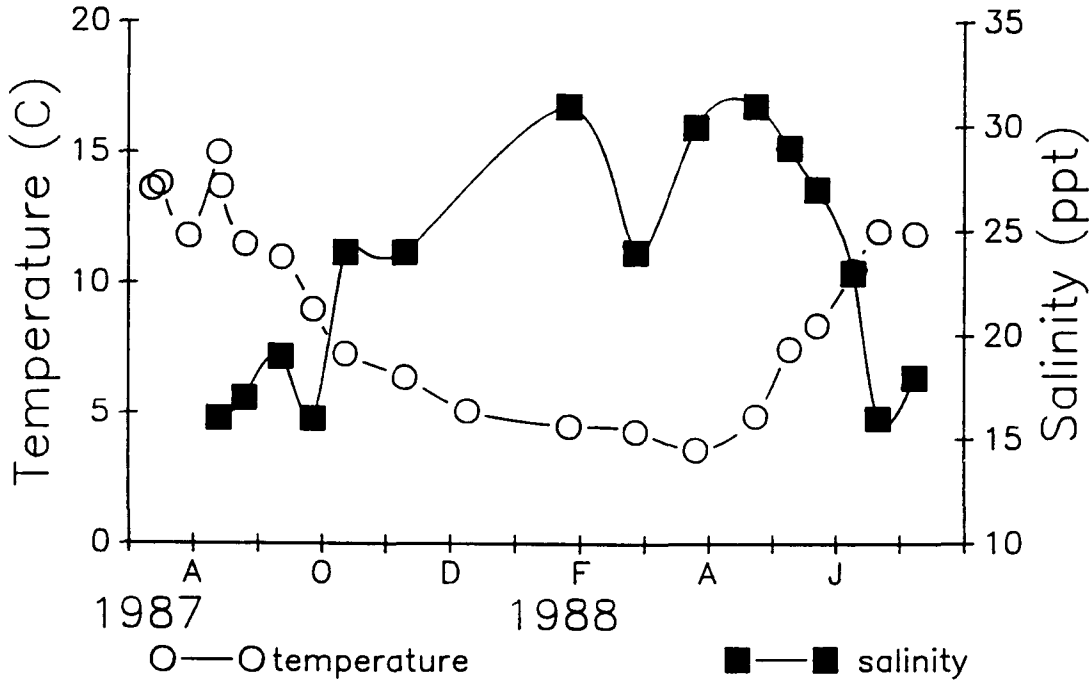

Figure 2. Water temperature (° C) and salinity values (°/oo) recorded at the study site in Auke Bay, Alaska during 1987 and 1988.

Faunal Composition

Nematodes and all life stages of harpacticoids comprised an average of 98.5% (± 1%) of the total number of meiofaunal organisms (Figure 3). Nematodes comprised 32 - 83% of the total number of meiofaunal organisms (x = 58.1% ± 3%). Harpacticoid copepods (adults and copepodites) were next in numerical abundance, comprising between 8 - 46% of total meiofauna (x = 24.5% ± 2%). Harpacticoid nauplii comprised 2 - 45% (x = 15.9% ± 3%). The other 1.5% of the fauna was cyclopoid copepods, calanoid copepods, barnacle nauplii and cyprid stages, bivalves, cumaceans, halocarid mites, ostracods, polychaetes, tardigrades, turbellarians, oligochaetes, isopods, and amphipods (Appendix B). While not all of these categories are considered "permanent meiofauna" (Higgins 1988), all were of meiofaunal size.

Seasonal Abundance

Meiofaunal densities from sample dates that appeared visually similar were grouped together and found to be statistically different (Kruskal Wallis; Appendix A). Strong seasonal trends in meiofaunal abundance were evident. Total meiofauna densities were highest on 13 May, 1987 (7043 · 10 cm $^{-2}$ ± 699), and declined rapidly to a low (1545 · 10 cm $^{-2}$ ± 458) on 10 July (Figure 4). Total meiofaunal densities remained low through 1 July, 1988 (the

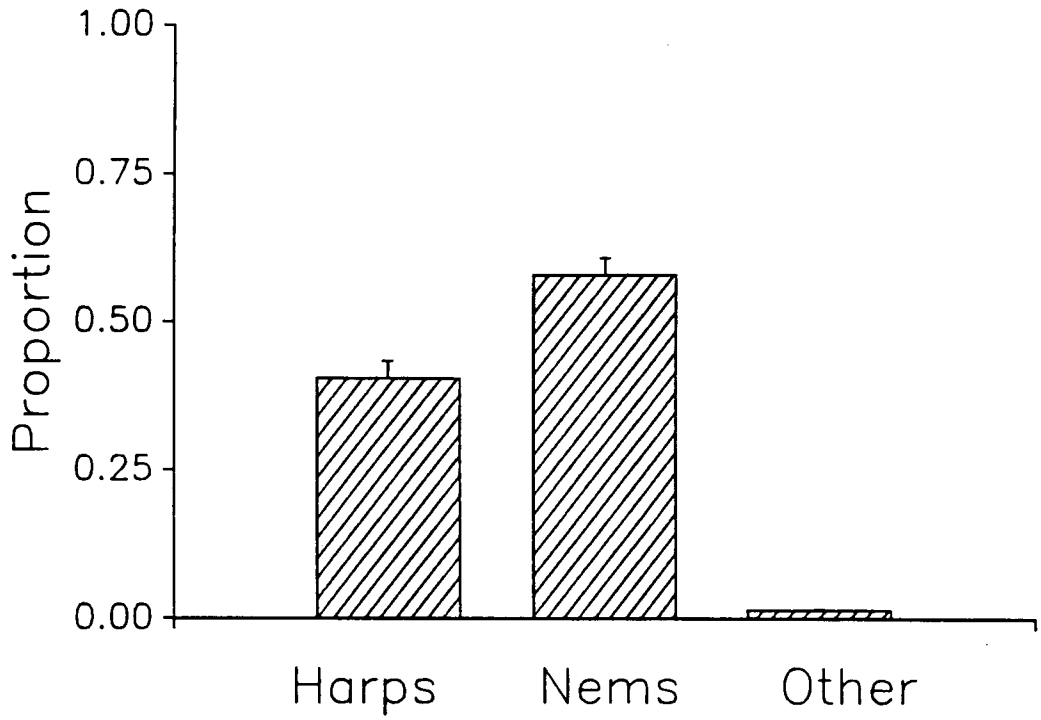

Figure 3. Total proportions of harpacticoid copepods of all life stages (Harps), nematodes (Nems), and other meiofauna from Auke Bay, Alaska for all sample dates combined. "Other" includes cyclopoid and calanoid copepods, barnacle nauplii and cyprids, bivalves, cumaceans, halocarid mites, ostracods, polychaetes, tardigrades, turbellarians, oligochaetes, isopods, and amphipods. Vertical bars represent one standard error.

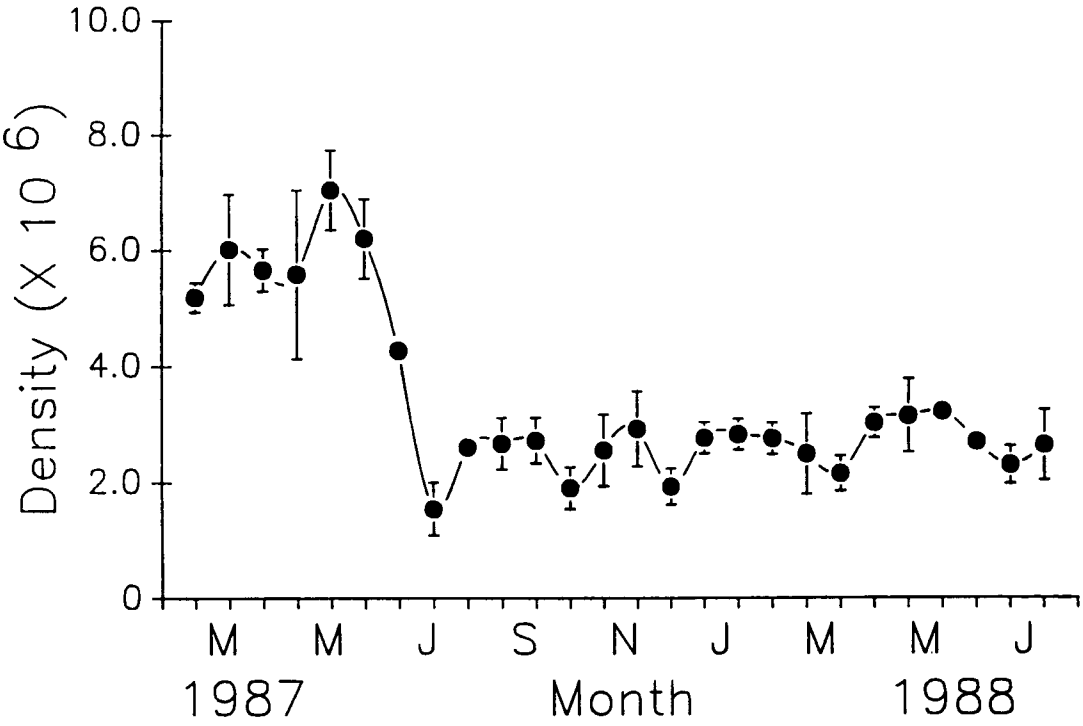

Figure 4. Average densities of total meiofauna (number/m^3) from Auke Bay, Alaska in 1987 and 1988. Meiofauna includes all life history stages of harpacticoid copepods, cyclopoid copepods, calanoid copepods, nematodes, barnacle nauplii and cyprids, bivalves, cumaceans, halocarids, ostracods, polychaetes, tardigrades, turbellarians, oligochaetes, isopods, and amphipods. Vertical bars represent one standard error.

end of sampling). Densities from March 22 - June 16 were significantly greater than during the remaining sample periods.

Harpacticoid copepods exhibited pronounced seasonal trends in reproduction and in abundance. Annual maximum densities of gravid female harpacticoids occurred on the first sampling date in March 1987 (115 · 10 cm^{-2} ± 22) and January, 1988 (159 · 10 cm^{-2} ± 27). The maximum proportion of gravid females to adult harpacticoids occurred in March of both years (Figure 5). The maximum density and proportion of gravid females were followed by rapid, significant decreases to low values in June and July of 1987 and 1988. The summer (June - August) of 1987 was characterized by low densities of gravid females, and low but gradually increasing proportions of gravid females to adult harpacticoids. Densities and proportions of gravid females on 1 July 1988 were not significantly different from those present in July 1987 collections.

Annual densities of harpacticoid nauplii were highest in April in 1987 and 1988 (Figure 6). In 1987 the maximum density occurred on 4 April (2864 · 10 cm^{-2} ± 638) with a rapid and significant decline to lower densities which persisted from 10 July through 5 November. In 1988 the maximum density occurred at nearly the same time as in 1987 (17 April) but was significantly lower than that in 1987

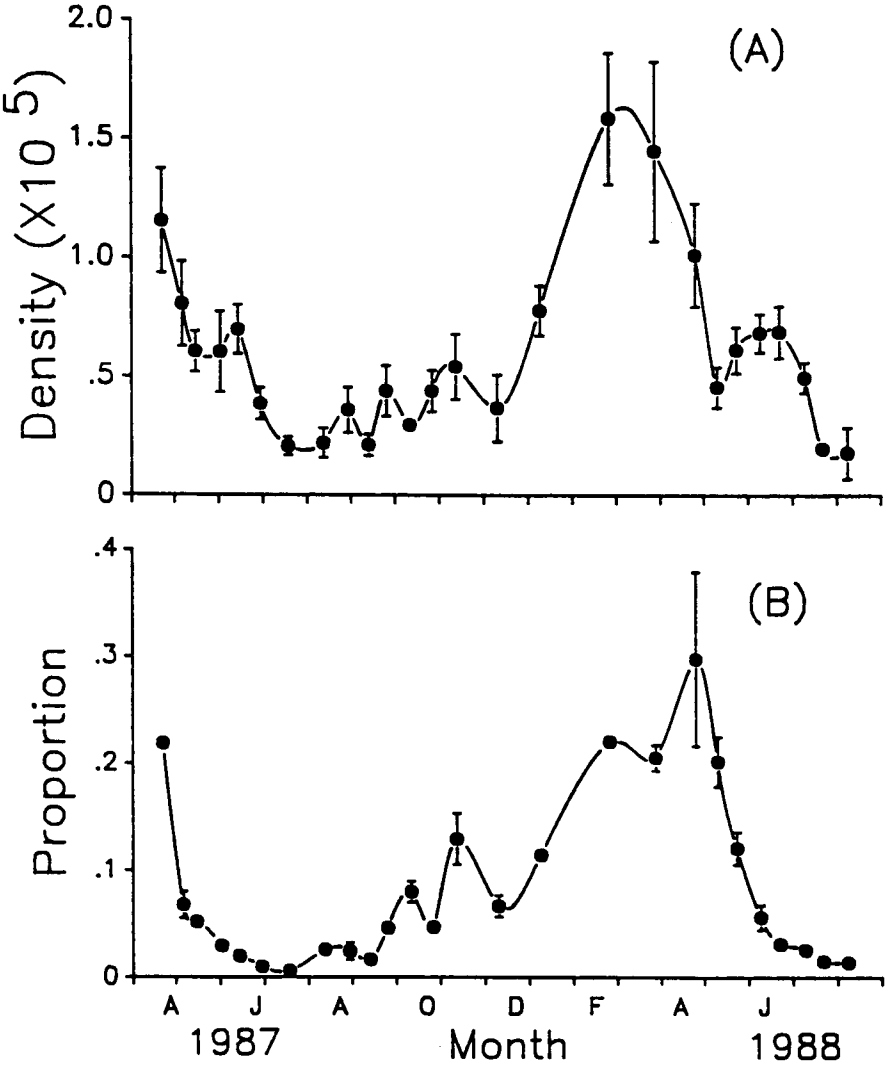

Figure 5. (A) Densities of gravid female harpacticoid copepods (#/m^3), and (B) proportions of gravid females to adult harpacticoids, from Auke Bay, Alaska in 1987 and 1988. Vertical bars represent one standard error.

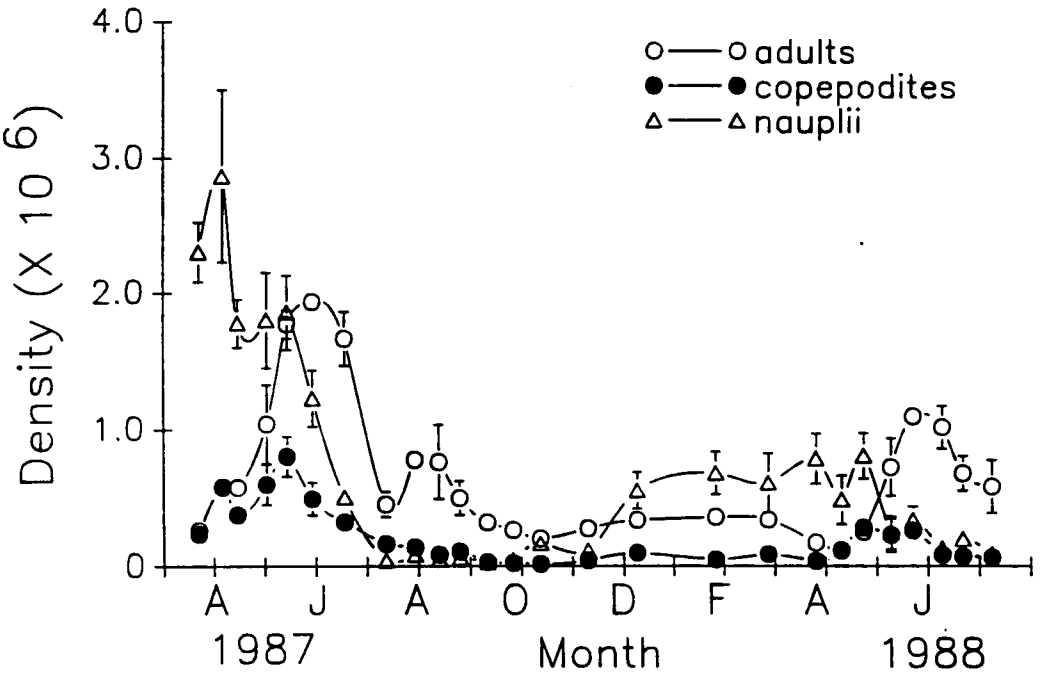

Figure 6. Average densities of harpacticoid nauplii, copepodites, and adults (#/m^3) from Auke Bay Alaska in 1987 and 1988. Vertical bars represent one standard error.

(808 ·10 cm $^{-2}$ ± 169). In both years, significant declines in the density of nauplii occurred after April, and summer densities were significantly lower than those occurring in late winter and early spring (December - March).

Densities of harpacticoid copepodites were highest in April and May during 1987 and 1988 (Figure 6). In 1987 the peak density (804 · 10 cm $^{-2}$ ± 148) occurred on 13 May, with a rapid decline to low numbers afterwards. The maximum density in 1988 occurred on 17 April and was significantly lower than the previous year (280 · 10 cm $^{-2}$ ± 44). Densities remained similarly high from 17 April - 16 May in 1988, after which a decline occurred to densities similar to those found in the corresponding period in 1987.

Trends in abundance of adult harpacticoids were similar for both years (Figure 6). Lowest yearly densities were recorded in March, followed by a rapid increase to peak densities which occurred on 28 May in 1987 (1935·10 cm $^{-2}$ ± 74) and on 16 May in 1988 (1099·10 cm $^{-2}$ ± 71). Densities declined rapidly and significantly thereafter in both years. Densities in 1987 were low from 7 September until the following April, when the 1988 spring increase began. Peak densities were significantly higher in 1987 than 1988.

The ratio of copepod nauplii to adults and copepodites has been used to identify reproductive trends for harpacticoid copepods (Shirley et al. 1988). Trends at the

study site were similar for both years. The ratio was highest in March (1987, 5.1 ± 0.1; 1988, 3.8 ± 0.1), followed by rapid declines to significantly lower values in May of both years (Figure 7). In 1987 the ratio began to increase in early October.

Nematodes had less seasonal changes in abundance than harpacticoid copepods (Figure 8). Nematode densities were significantly higher from 22 March - 28 May, 1987, than on any other sample date. The peak density (2852 · 10 cm^{-2} ± 390) occurred on 14 April, 1987. A slight but insignificant increase in density also occurred in the fall of 1987. The highest density for 1988 occurred in early May (1935 · 10 cm^{-2} ± 225), but this was not significantly different than other dates. The lowest annual densities occurred in June - early July in both 1987 (857 · 10 cm^{-2} ± 299) and 1988 (1324 · 10 cm^{-2} ± 222); however, these densities were not significantly different than other dates.

A few other taxa had seasonal trends in abundance, but there were no significant differences in densities between sample dates (Appendix B). Few specimens of minor taxa were collected overall and the groups comprised a small percentage of the total meiofauna (Figure 3). Barnacle nauplii and cyprids, turbellarians, and bivalves were collected up to a month earlier in 1988 than 1987. Barnacle nauplii were collected between 14 April - 10 July, 1987, and

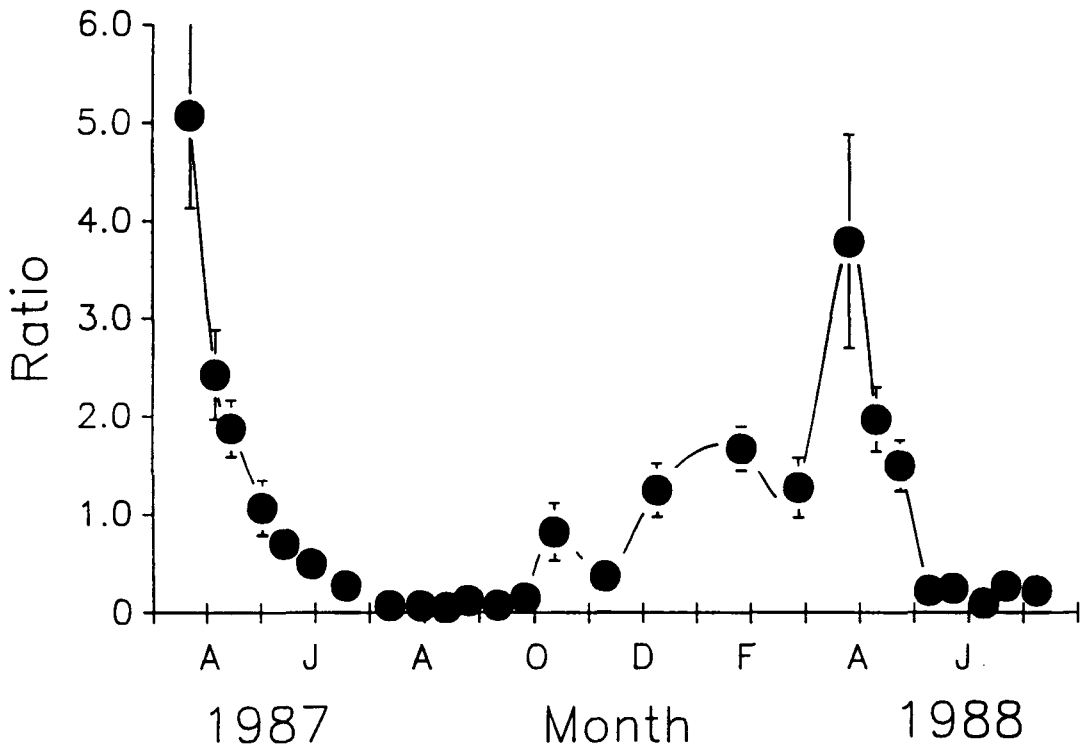

Figure 7. Average ratios of harpacticoid copepod nauplii to adults and copepodites from Auke Bay, Alaska for 1987 and 1988. Vertical bars represent one standard error.

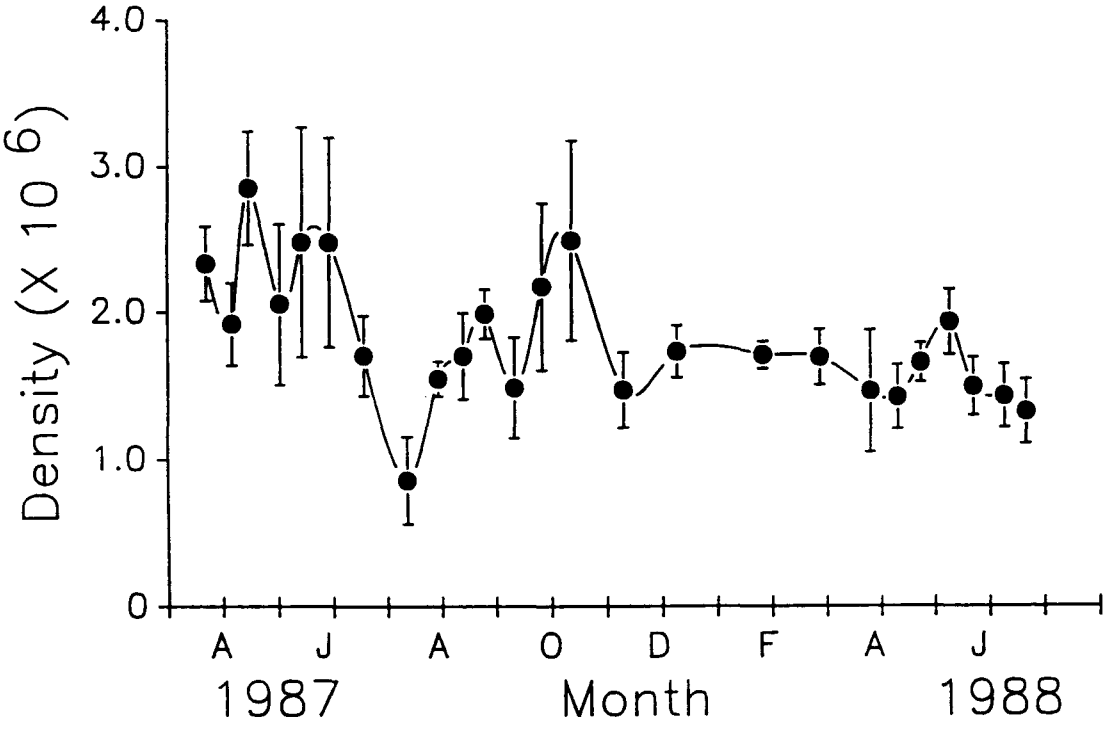

Figure 8. Densities of nematodes (#/m ^{3}) from Auke Bay, Alaska for 1987 and 1988. Vertical bars represent one standard error.

20 March - 16 May, 1988. Turbellarians were present from 13 May - 16 June, 1987, and from 17 April - 14 June, 1988. In 1987 barnacle cyprids were collected only on 16 June. In 1988 cyprids were collected from 16 May - 1 July. Bivalves were first collected on 16 June, 1987, and continued to be present in samples in low numbers through 8 October. In 1988, bivalves were collected from 2 June - 1 July.

Juvenile and adult polychaetes were primarily present in the spring and summer, between mid-April and late August in 1987, and from mid-April to 1 July in 1988. No seasonal trends in abundance were found for cyclopoid copepods or halocarid mites, but both groups were present in low densities during nearly every sample period. Oligochaetes were present only in samples from 22 March - 13 May, 1987, and none were found in 1988.

Discussion

Harpacticoid reproduction followed a seasonal cycle in both 1987 and 1988. The density of gravid females was highest during the first sampling period of each year: in March, 1987 and January, 1988. The 1987 peak probably occurred prior to the beginning of my study. The density of nauplii was highest in April of 1987 and 1988; that of copepodites was highest from mid-April to mid-May of both years, and the density of adult harpacticoids was highest in mid-to late May of both years.

An apparent anomaly in the density data of the life history stages of harpacticoid copepods is that there were more adult copepods than copepodites. Several plausible explanations exist for this. An accumulation of adults would occur if the amount of time harpacticoids spent as adults was longer than the time spent as juveniles. It is also possible that copepodites were misidentified as adults. Less likely explanations would be that adult harpacticoids from other areas may have colonized the study site during spring, or copepodites could have been advected to other areas.

While the timing of reproduction was similar between years, the magnitude of the harpacticoid population was considerably less in 1988 than in 1987. Great variation in densities between years is common for meiofauna (Coull

1985). The maximum densities of nauplii were more than three times greater in the spring of 1987 than in 1988. The densities of copepodites were approximately 2.5 times greater in 1987 than in 1988 and the peak density of adult harpacticoids was nearly two times greater the first year than the second. Survival or production of all life stages of harpacticoids was negatively affected by some factor or factors during 1988.

Temperature may affect fecundity and rates of development in harpacticoids (see Hicks and Coull 1983 for review). The majority of reproduction in Auke Bay occurred during the coldest months of the year (January - March). If reproduction was temperature dependant, colder temperatures could have resulted in the production of fewer nauplii. However, this does not appear to be the situation in the intertidal area of Auke Bay. Sea surface temperatures from January through March averaged 3.96° C in 1987, and 4.54° C in 1988 (Dr. Bruce Wing, National Marine Fisheries Service Auke Bay Laboratory, personal communication). Despite colder winter temperatures in 1986 - 1987 than in 1987-1988, far more nauplii were produced in 1987 than in 1988. Warmer water temperatures may speed development and cause hatching to occur earlier. Nauplii that hatch early in the season may miss important food sources, similar to the match-mismatch hypothesis proposed by Cushing (1975) for fish

larvae. Maximum densities of copepodites and adult harpacticoids occurred nearly two weeks earlier in 1988 than in 1987. Possibly survival was poorer in 1988 because hatching did not coincide well with the production of food. This, in addition to the production of fewer nauplii, could have resulted in a lower maximum density of adult harpacticoids in 1988 than in 1987.

Reproduction of intertidal harpacticoids in Auke Bay may be food, rather than temperature, limited. In Auke Bay the spring phytoplankton bloom appears to be a predictable, annual event in response to increased light intensity rather than to increases in temperature (Ziemann et al. 1988). High latitude systems, including Auke Bay, are typically uncoupled; that is, a substantial portion of the pelagic primary production is not immediately consumed by pelagic herbivores, but rather sinks uneaten to the benthos. Subtidally, the timing of harpacticoid reproduction appears to be related to the bloom sedimentation event for two of the three major species in Auke Bay (Fleeger and Shirley in press). Fecundity and rates of development for several species of harpacticoids are affected both by quantity and quality of food (see Hicks and Coull 1983 for review). Meiofaunal reproduction in intertidal areas of Auke Bay may be triggered by food availability.

Despite cold temperatures, the combination of a food-

rich environment and a lack of predators might make winter a desirable time of year for harpacticoids to reproduce. Other studies have suggested that the development of meiofaunal food in winter may lead to concomitant increases in the meiofauna (Coull 1985) or that the accumulation of phytoplankton detritus in the sediment during winter may lead to springtime increases in the benthos (Rudnick et al. 1985). Little is known concerning fall blooms in Auke Bay (Shirley and Coyle 1986). Low densities of harpacticoids and other meiofauna in the fall and winter may allow detrital food resources from such events to accumulate in the sediment. In addition, fish and invertebrate predators of meiofauna are largely absent from intertidal areas during this time (personal observation). More detailed study of the diets of intertidal harpacticoids, the effects of temperature extremes, and the presence of potential predators, are required for understanding of year to year fluctuations in density.

Harpacticoids were second in overall numerical abundance and approached the density of nematodes in May and June of 1987 and 1988, but never exceeded it. Typically, in marine sediments nematodes rank first in terms of the total density, and harpacticoid copepods are usually the second most abundant taxon. Medium to fine sands and muds are regularly dominated by nematodes, with harpacticoids

becoming numerically more important with increasing sediment grain size (Hicks and Coull 1983). Many other factors can affect the density and distribution of harpacticoids, such as sediment chlorophyll concentrations (Pfannkuche and Thiel 1987), wave and/or current intensity (Coull 1970), the temperature and oxygen concentration of interstitial waters (Coull 1970; McLachlan et al. 1977; Dye 1978 a,b), or the density of macrofaunal or epibenthic predators (Fitzhugh and Fleeger 1985; Palmer 1988; Coull et al 1989), all of which may vary seasonally. The mechanisms that regulate meiofaunal seasonal patterns are complex, interactive, and not easily discernible (Coull 1985).

Predation may play an important role in regulating the density of harpacticoids at the study site. Harpacticoids are abundant in the diets of many larval and juvenile fish but the effect of predation on the density of harpacticoids has been the subject of much disagreement. Some studies suggest that predation may cause fluctuations in harpacticoid densities (Feller and Kaczynski 1975; Morais and Bodiou 1984; Coull 1985; Fitzhugh and Fleeger 1985). Others have suggested that the predation pressure exerted on harpacticoids is negligible (McIntyre and Murison 1973; Sibert et al. 1977; Alheit and Scheibel 1982; Hicks 1985). In Auke Bay, intertidal harpacticoid densities declined dramatically after attaining a maximum in May. Many

juvenile fish known to prey on harpacticoids, such as salmon fry (Feller and Kaczynski 1975; Landingham 1982; Cordell 1986) and several species of flatfish (Hicks 1984; Sturdevant 1987; McGregor chapter 2) utilized the nearshore environment during this time. Salmon fry outmigrated from many nearby creeks beginning in March (Mortensen and Wertheimer 1988). Juvenile starry flounder and rock sole settled out of the water column in intertidal areas beginning in June. I collected these species, plus many others of similar sizes, during spring and summer from the study site concurrently with the meiofauna samples (McGregor chapter 2). A significant decline in the density of harpacticoids occurred at the same time as this influx of juvenile fish and invertebrates and should be evaluated for possible predation-caused reductions in density.

Nematode densities varied greatly between cores within sampling dates throughout the study. Such variation is not uncommon (Fleeger and Decho 1987; Fleeger et al. 1989) and may be attributed to many factors. Nematodes have wide vertical zonation, and their depth distribution may vary with season, with tidal stage, or diurnally (see Hicks and Coull 1983 for review). Competition (Coull and Fleeger 1977; Hicks and Coull 1983) and predation or disturbance (Coull and Palmer 1984; Coull et al. 1989) can also affect the distribution of meiofauna. A patchy distribution may

result in variable densities between cores.

Barnacle nauplii and cyprid stages, bivalves, and polychaetes were examples of temporary meiofauna and were collected only in spring and summer, after which they probably grew too large to pass through the 0.500 mm mesh sieve. The appearance of barnacle nauplii and cyprids and bivalves earlier in 1988 than in 1987 may have been due to the effects of warmer water temperatures on rates of development. Seasonal trends were not apparent for other meiofaunal organisms which were found in low densities (cyclopoid copepods, halocarid mites, ostracods, tardigrades, turbellarians, isopods, amphipods). Several representatives of pelagic or epibenthic zooplankton were occasionally collected (calanoid copepods, cumaceans). Oligochaetes, only present early in 1987 (March - May) may have been responding to factors similar to those responsible for the high numbers of harpacticoids and nematodes at the same time.

There has been little previous study on intertidal meiofauna populations in Alaska (Feder and Paul 1980; Landingham 1982; Cordell 1986). Many commercially important fish and invertebrate species utilize Alaskan intertidal areas as juveniles and are dependant upon meiofauna, especially harpacticoid copepods, as a primary food resource (Landingham 1982; Cordell 1986; Sturdevant 1987; McGregor

chapter 2). The study of seasonal patterns in meiofaunal community composition and density are important in order to understand the early life histories of commercially valuable species. Few studies address the uptake of meiofauna by predators in relation to the available food supply (Gee 1989). Such studies can be useful in determining whether food limitation might be a factor in the survival of early post-metamorphic fish and invertebrates, and whether predation might have a significant influence on harpacticoid populations. This study, and the companion study on the role of meiofauna in the diets of post-metamorphic flatfish (McGregor chapter 2), suggest that harpacticoid copepods are a vital food resource to some species that utilize the nearshore areas as juveniles, and that the availability of harpacticoids may be important to the survival of those predators most dependant upon them.

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CHAPTER II.

SEASONAL AND ONTOGENETIC CHANGES IN THE IMPORTANCE OF MEIOFAUNA IN THE DIETS OF POSTMETAMORPHIC FLATFISH

I. INTRODUCTION

Pleuronectid fish undergo great physiological and behavioral changes at metamorphosis, including settlement from the pelagic zone to a demersal environment and switching to benthic prey. The postmetamorphic period may be a critical phase in the early life histories of flatfish. For most fish, survival through the larval period is thought to be dependant on spatial and/or temporal distribution of larvae relative to that of their prey populations (Cushing, 1975; Hjort, 1914; Lasker, 1981). A similar critical period of prey availability may occur at the time of settlement for flatfish.

Meiofauna, especially harpacticoid copepods, are preyed upon by many juvenile fish. Some authors have suggested that a diet composed only of meiofaunal prey was not sufficient, and that energy derived from macrofaunal prey was necessary to sustain growth of fish (Bregneballe, 1961). Other studies have found that the diets of small juvenile fish were comprised primarily or entirely of meiofaunal prey (Alheit and Scheibel, 1982; Morais and Bodiou, 1984; Hicks, 1984; Hogue and Carey, 1982). These studies suggested a "critical length" at which fish switched from a diet composed primarily of harpacticoids to one of small macrofauna. This length has been estimated at 30.0 mm (Hicks, 1984) to 40.0 mm (Alheit and Scheibel, 1982). Most

recently, Shirley et al. (1987) found that a diet composed entirely of harpacticoids provided sufficient energy for growth in starry flounder (Platichthys stellatus) less than approximately 28.0 mm in length.

Few attempts have been made to examine the seasonal abundances of prey species in relation to seasonal presence of their predators. The diet of juvenile English sole (Parophrys vetulus) was a function of size, location of capture, and season in a study by Hogue and Carey (1982). Within-year and between-year differences in diet were thought to be related to changes in the density of prey organisms. The period of maximum density of harpacticoids coincided with their maximum occurrence in the diets of postmetamorphic english sole. Flatfish consumed large numbers of the harpacticoid Parastenhelia megarostrum and were assumed to be responsible for reductions in densities of the copepod in a study by Hicks (1984). However, continuous reproduction and recruitment by P. megarostrum were thought to enable the population to sustain the variable levels of predation imposed throughout the year.

Auke Bay, Alaska provides an excellent area for the study of juvenile flatfish and their prey. Auke Bay is a rearing area for the larvae and juveniles of over 25 species of fish, including six species of pleuronectids (Haldorson et al., 1989). Some pleuronectid fish, such as flathead

sole (Hippoglossoides elassodon) utilize offshore subtidal habitats even as newly metamorphosed juveniles, while others settle in nearshore environments. Several species may jointly inhabit the intertidal zone at certain times of the year, resulting in either competition for, or sharing of, resources. An intertidal area within the bay was utilized by several species of juvenile pleuronectids during the spring of 1986, and these fish fed to differing degrees on meiofauna (Sturdevant, 1987). I sought to compare the food habits of pleuronectid fish species inhabiting the nearshore environment, and to describe ontogenetic changes in diets. I hypothesized that the diets of similar sized fish were most similar to one another, and that metamorphosis coincided with the highest abundances of harpacticoid copepods.

II. METHODS AND MATERIALS

Study Area

Auke Bay is located in southeastern Alaska, near Juneau (Figure 1). The bay is approximately 16 km ^{2} in area, 70% of which is less than 60 m in depth. The substrate is primarily mud. The glacial Mendenhall River flows into ajoining Fritz Cove, approximately 2 km to the southeast. See Shirley and Coyle (1986) for a complete description of Auke Bay.

Fish were collected from a cove located on the east side of Auke Bay (Figure 1). The upper intertidal zone and entire south side of the cove grade from a zone inhabited by Mytilus edulis to a barnacle-inhabited Fucus sp. zone. In the north end of the cove, a small patch of eel grass, Zostera marina, is present above, and a mudflat of silty clay begins below, the 0 m tidal level. Fish were collected from the mudflat, an area approximately 60 m wide and exposed at minus tidal levels. Water temperatures and salinity were measured when samples were collected. Water temperatures (°C) were recorded at the sample site using a Digi-sence Thermocouple Thermometer. A water sample was collected and upon return to the lab, salinity was measured (°/oo) with an ATAGO refractometer. During the study, water temperatures varied from 3°C in winter to 15°C in summer, and salinity varied from 16 to 31 °/oo (Appendix C).

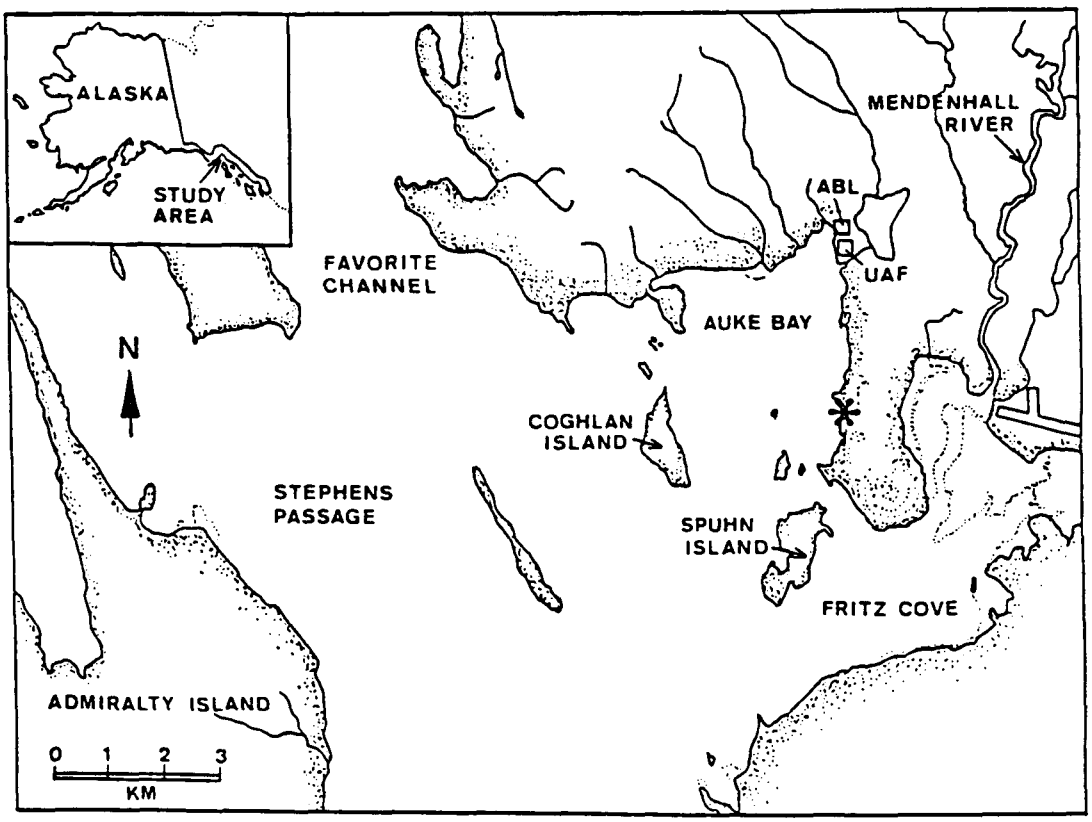

Figure 1. Study area in Auke Bay, Alaska. Asterisk marks collection site.

Sampling Procedure

Samples of fish and meiofauna were collected concurrently, at two week intervals from July through October, 1987, monthly throughout the winter, and again at two week intervals from March through June, 1988, totalling 19 sampling periods over the 12 month period (Appendix A). Collections were made on the lowest tides of the cycle.

Fish were collected by hand-deploying a beach seine (17 X 2 m in dimension, 6 mm stretch mesh). A maximum of ten seine hauls were made on each sample date in an attempt to collect 20 fish of all species combined. Fish were anaesthetized with tricain methanesulfonate (MS222) to prevent regurgitation of stomach contents, then preserved in a 10% buffered formalin solution. Fish were measured (standard length) a minimum of 30 days after collection, to the nearest 0.5 mm. The stomachs were dissected and prey items were counted and identified to major taxon at the same time.

Each fish species was divided into three size classes for analysis: small (less than 20.0 mm), medium (20.0-34.5 mm), and large (35.0 mm and greater). Preliminary investigation indicated that these were the approximate lengths at which fish were switching prey types.

Up to one hundred intact prey specimens were chosen from stomach contents for determination of average prey

weights. Since weights were obtained from partially digested prey (and so were probably not accurate estimations of actual prey weights) I calculated proportions of total weight for each prey category. Proportional weight estimations are better measures of the energy provided by different prey groups than comparisons of numerical proportions. However, Nishiyama and Hirano (1983) stated that average weights do not take into consideration variations in size (and thus weight) of conspecific prey items. Fish switched from a diet composed primarily of meiofauna to one of primarily small macrofauna at approximately 35.0 mm. However, some prey groups were taken by fish of all sizes. To compensate for variations in the sizes of these prey categories, I calculated average weights for prey from fish less than 35.0 mm in length, and from fish greater than 35.0 mm. Average dry weights for each prey category were estimated by weighing groups of prey on a Cahn electrobalance 4700 after drying the prey groups for 24 hours at 69 °C.

Statistical Analysis

Twelve categories of prey were analyzed, including one group consisting of rare or unidentifiable prey which were lumped together in an "other" group (Table 1). Frequency of occurrence, and mean percentage of the total diet by number

and by weight were calculated for each major prey group and were compared among fish groups by Kruskal Wallis tests. Where significant differences were indicated, Mann-Whitney pairwise tests were used to detect where the differences existed (Conover, 1980). Differences were considered statistically significant with a probability level of less than 0.05, and highly significant with a probability level of less than 0.01. Statistical analysis were performed using Statgraphics (Statistical Graphics Corp., 1986).

Total diets were compared between groups with prey categories expressed both as proportion by number and by weight. The use of proportions is preferable when unequal sampling efforts disallow direct comparison of absolute abundance data (Boesch, 1977). Several authors have suggested different feeding rhythms for juvenile flatfish. Flounders in the lab searched for food at dusk and at dawn in a study by Bregneballe (1961). The stomachs of four species of flatfish were emptiest before 0900 hrs, and fullest at 1800 hrs, in a study by Hogue and Carey (1982). Sturdevant (1987) found that starry flounder stomachs were also fullest in the evening (1830) and that the maximum number of empty stomachs occurred at midnight. Food intake of starry flounder is also reported to be greatest during the highest tides (Campana, 1984). I collected fish at different times of the day, but consistantly on the lowest

Table 1. Sample sizes of rock sole, starry flounder, and yellowfin sole collected during 1987-1988 in Auke Bay, Alaska.

Species	Small	Medium	Large	Total
Rock sole	26	19	5	50
Starry flounder	42	12	50	104
Yellowfin sole	26	57	28	111
Total	94	88	83	265

tides of the cycle to coincide with meiofauna collections (McGregor, chapter 1). I did not investigate stomach fullness, but assumed that fish may have contained different amounts of prey, so diets were standardized by comparing proportions of prey types rather than absolute numbers or weights of prey. Comparisons of total diets were made using the Spearman Rank Order Correlation Coefficient (SCC or rho statistic), calculated as:

$$SCC_{jk} = 1-[(6\ \sum(R_{ij}-R_{ik})^2)/(N/(N^2-N))]$$

where R_{ij} or R_{ik} is the rank of prey variable i in fish species j or k, and N is the number of pairwise comparisons. Correlation coefficients range from -1 (completely dissimilar) to +1 (completely similar).

The Spearman Rank Order Correlation Coefficient has been used previously to test for correlation between pairs of fish diets (Fritz, 1974; Sturdevant, 1987). Measures of rank correlation are useful when data depart significantly from the normal distributions on which parametric tests are based. The Spearman rho statistic has the advantage of being applicable to various types of percentage data (Fritz, 1974) and can be used to test hypotheses of correlation (Conover, 1980). For this study a two-tailed test was used to test the following hypotheses:

Ho: Pairs of fish diets (X_i,Y_i) were mutually independent;

Ha: Either there was a tendancy for larger X and Y values (fish diets) to be paired, or there was a tendancy for smaller X values to be paired with larger Y values.

Multivariate Statistical Package (MVSP; Kovach, 1986) was used to calculate the Searman rank correlation coefficient.

The measures of dietary similarity were clustered by multivariate numerical classification techniques, with entities (fish groups) grouped based on the resemblances of their attributes (prey types). The SCC distance measures were sorted by combinatorial cluster analysis using an unweighted pair group method-average (UPGMA; Boesch, 1977). MVSP (Kovach, 1986) was used to perform cluster analysis.

III. RESULTS

Fish collection

Totals of 55 rock sole, 121 starry flounder, and 125 yellowfin sole were collected over the sampling period. Only fish with food in their stomachs were used for analysis, reducing sample sizes to 50 rock sole, 104 starry flounder, and 111 yellowfin sole (Table 1). By size class, collections totaled 96 small fish, 93 medium fish, and 85 large fish, of which 94 small (including 26 rock sole (rs), 42 starry flounder (sf), and 26 yellowfin sole (ys)), 88 medium (19 rs, 12 sf, 57 ys), and 83 large (5 rs, 50 sf, 28 ys) were used for analysis (Appendix D).

Prey Composition

Prey items consumed by all species and size classes of fish were almost entirely benthic or epibenthic meiofauna, or small macrofauna (Table 2). All three fish species consumed at least small proportions of all prey categories. Neither rock sole nor yellowfin sole fed heavily on mysids; only one medium and one large rock sole, and one large yellowfin sole ate mysids. Whole bivalves were eaten by only one large starry flounder; only one small starry flounder consumed ostracods; cyprids were consumed by only two small starry flounder. Harpacticoids, ostracods, and halocarid mites were the only prey items considered to be permanant meiofauna (holomeiofauna); however, other

Table 2. Prey categories for rock sole, starry flounder, and yellowfin sole. Abbreviations are used in all following tables and figures. The "other" category includes loose copepod ovisacs, calanoid copepods, chironomid larvae, cumaceans, eggs, fish larvae, gastropods, crab glaucothoe, halocarid mites, and nematodes.

Category	Abbreviation
Harpacticoid copepod	HA
Cyclopoid copepods	CY
Copepod nauplii	NP
Amphipods	AM
Appendicularians	AP
Bivalves (whole)	BV
Bivalve siphons	BS
Barnacle cyprids	CP
Mysids	MY
Ostracods	OS
Polychaetes	PO
Other	OT

categories might be considered temporary meiofauna, such as polychaetes (Higgins, 1988).

Stomach Content Analysis

Prey categories are described as being of primary importance in the diet, of secondary importance, or as contributing little to the diet. A primary prey category is one which 1) had a greater than 0.60 frequency of occurrence; 2) constituted greater than 20% of the diet numerically; and 3) constituted greater than 20% of the diet by weight. A secondary prey category is one which 1) had a greater than 0.15 frequency of occurrence; and 2) constituted greater than 10% of the diet either numerically or by weight. Prey categories mentioned as being of little importance to the diet constituted less than 10% of the diet numerically and by weight, but had a frequency of occurrence greater than 0.10. Prey categories not mentioned had a frequency of occurrence less than 0.10 and contributed less than 10% of the diet both numerically and by weight.

The diet of small rock sole consisted primarily of harpacticoid and cyclopoid copepods. Copepod nauplii, appendicularians, ostracods, bivalves, bivalve siphons and polychaetes were preyed upon by 11 - 15% of fish of this size class (Figure 2), but contributed little to the diets numerically or by weight (Figure 3). Diets of medium rock

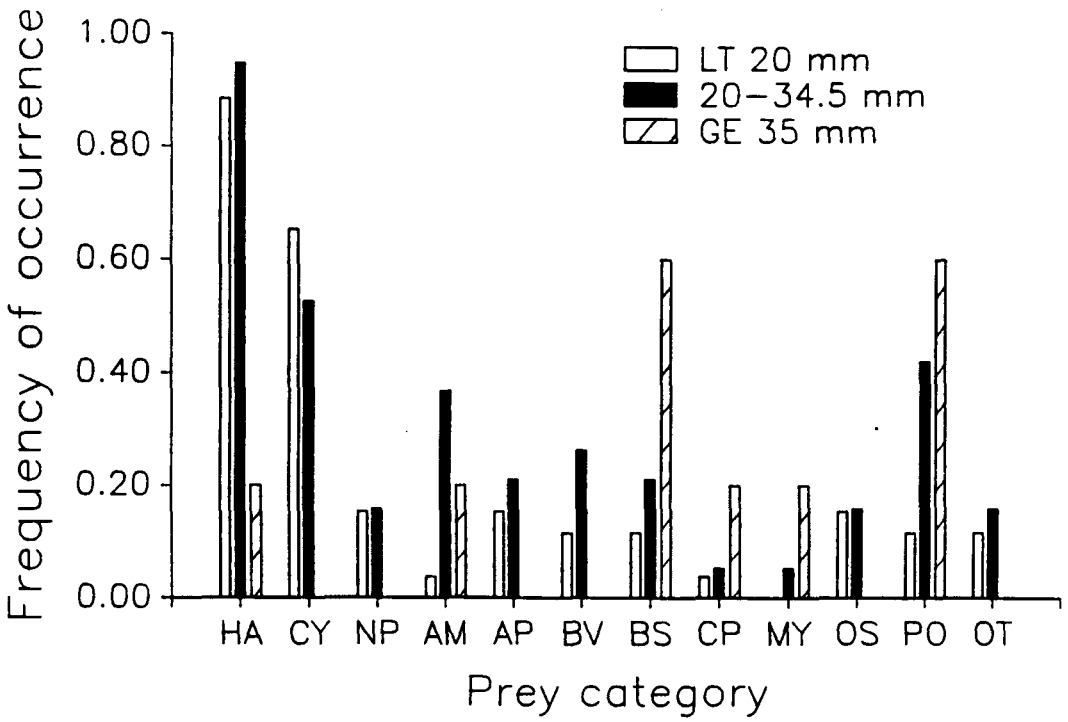

Figure 2. Frequencies of occurrence of prey categories from rock sole of: A) less than 20.0 mm, B) 20 - 34.5 mm, and C) 35.0 mm and larger, standard length. Prey categories are abbreviated as in Table 2.

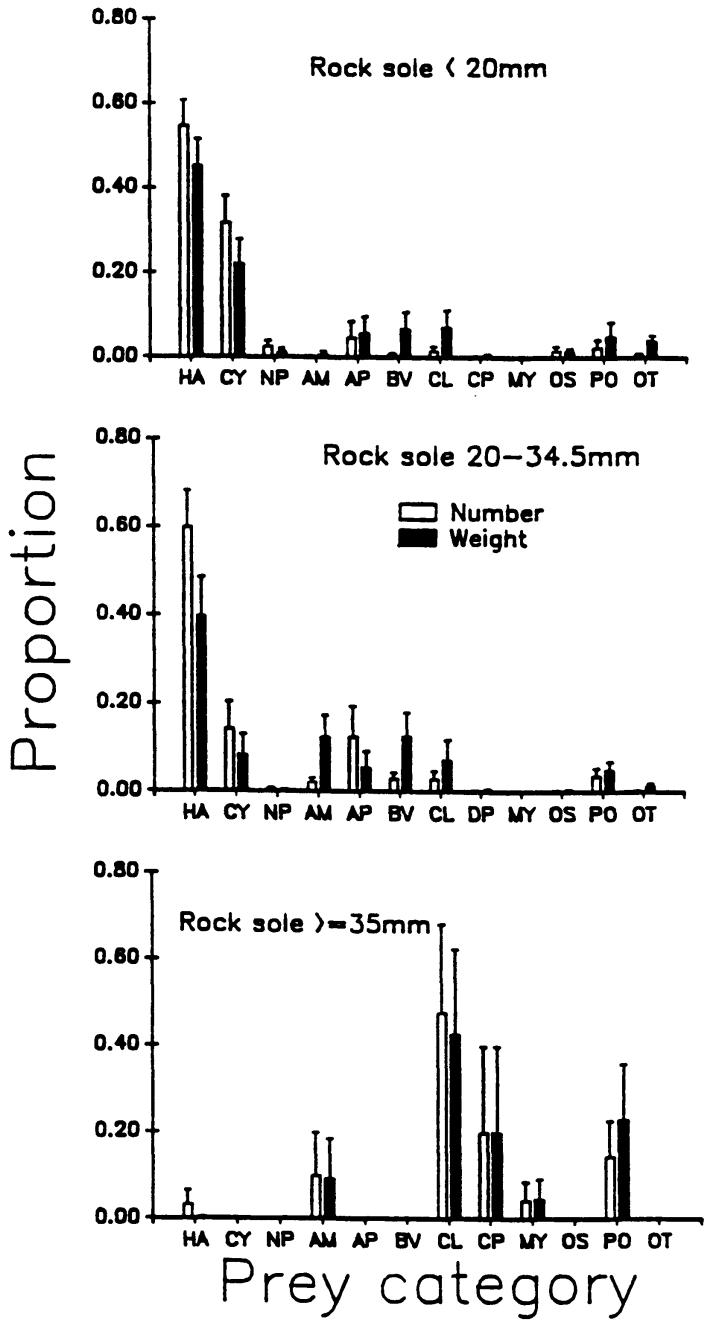

Figure 3. Proportion by number and weight of prey categories from rock sole of: A) less than 20.0 mm, B) 20.0 - 34.5 mm, and C) 35.0 mm and larger, standard length. Prey categories are abbreviated as in Table 1. Vertical bars represent one standard error.

sole contained predominantly harpacticoid copepods. Prey groups of secondary importance were cyclopoid copepods, amphipods, appendicularians, and whole bivalves. Copepod nauplii, ostracods, bivalve siphons and polychaetes were consumed by 42 - 16% of the fish (Figure 2), but contributed little to the diets numerically or by weight (Figure 3).

Data for large rock sole are based only on five fish. The diet of one fish consisted of only one barnacle cyprid. Therefore the proportional contributions of cyprids to the diet of this size class of rock sole are probably artificially high, and other prey categories correspondingly too low. Large rock sole diets consisted primarily of bivalve siphons (Figure 3). Polychaetes, amphipods, and cyprids, each contributed secondarily to the diet. Mysids were also consumed by 20% of the fish, but contributed little to the diet by weight (Figure 2).

Small starry flounder fed primarily on harpacticoid copepods. Cyclopoids and copepod nauplii were found in the stomachs of 27% and 22% of fish of this size class (Figure 4), but contributed little to the diets numerically or by weight. The primary prey of medium starry flounder was also harpacticoid copepods. Amphipods and mysids were prey categories of secondary importance (Figure 5). Although cyclopoid copepods were consumed by 24% of fish of this size class (Figure 4), they were a small proportion of the diet

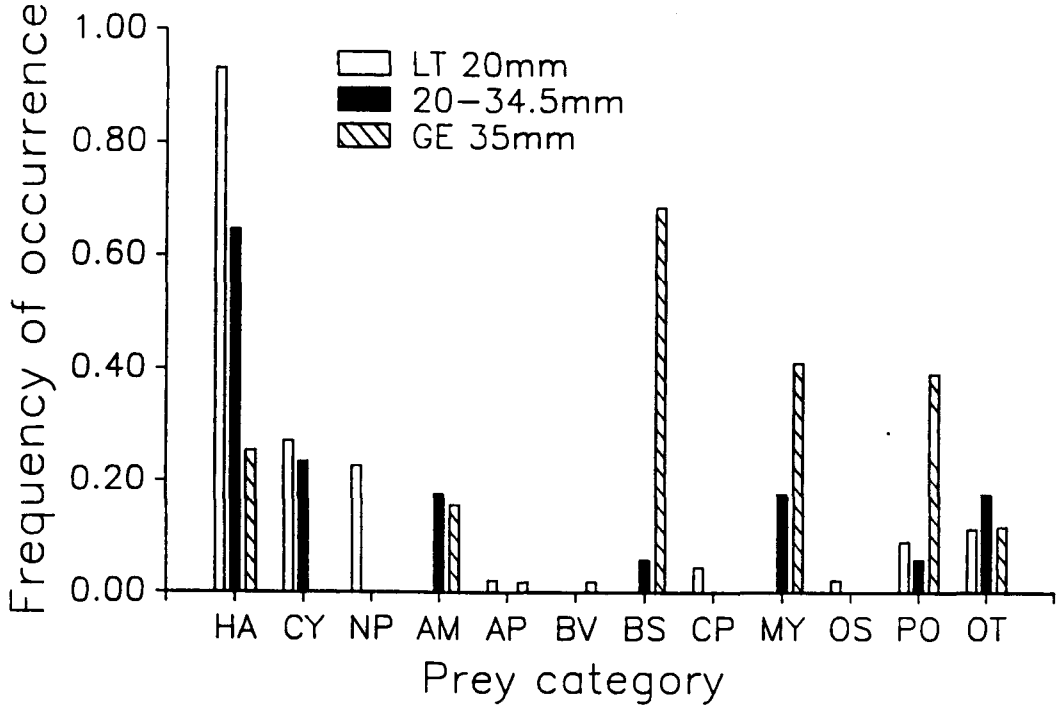

Figure 4. Frequencies of occurrence of prey categories from starry flounder of: A) less than 20.0 mm, B) 20.0 - 34.5 mm, and C) 35.0 mm and larger, standard length. Prey categories are abbreviated as in Table 2.

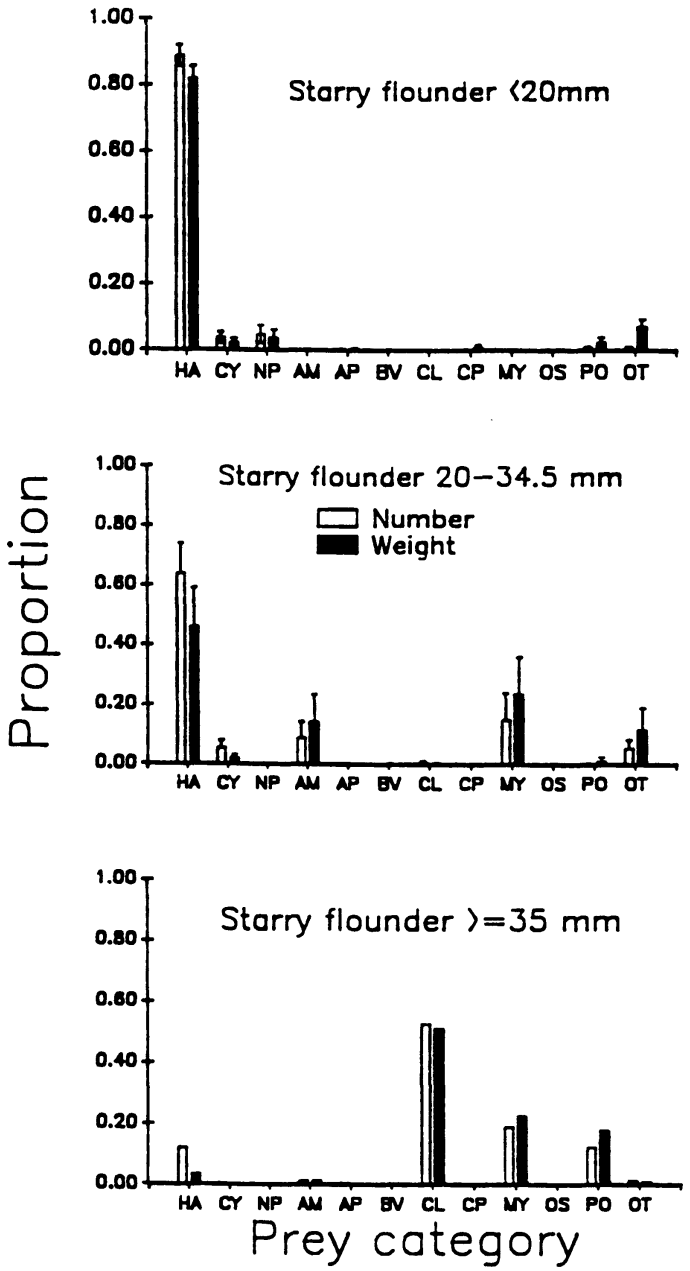

Figure 5. Proportion by number and by weight of prey categories from starry flounder of A) less than 20.0 mm, B) 20.0-34.5 mm and C) 35.0 mm and larger, standard length. Prey categories are abbreviated as in Table 1. Vertical bars represent one standard error.

by number and by weight. Bivalve siphons were the primary prey of large starry flounder. Mysids, polychaetes, and harpacticoid copepods were secondary prey (Figure 5). Amphipods were eaten by 16% of large starry flounder, but contributed little to the diet numerically or by weight.

Small yellowfin sole fed primarily on harpacticoid copepods. Copepod nauplii and cyclopoid copepods were found in the stomachs of a majority of small yellowfin (Figure 6), and these prey types contributed secondarily to the diets. Harpacticoids were also the major prey for medium yellowfin sole. Polychaetes and bivalve siphons were of secondary importance in the diets (Figure 7). While 44% of medium yellowfin sole consumed copepod nauplii and 37% consumed cyclopoids (Figure 6), neither contributed over 1% of the diet numerically or by weight. Amphipods were consumed by 16% of medium yellowfin sole but contributed little to the diet. Large yellowfin sole fed on a greater range of prey categories than similar sized rock sole or starry flounder. The primary prey items were bivalve siphons. Secondary prey items were harpacticoid copepods, whole bivalves, and polychaetes (Figure 7). Amphipods, barnacle cyprids, and ostracods were each found in the stomachs of more than 10% of large yellowfin sole (Figure 6) but contributed little to the diet numerically or by weight (Figure 7).

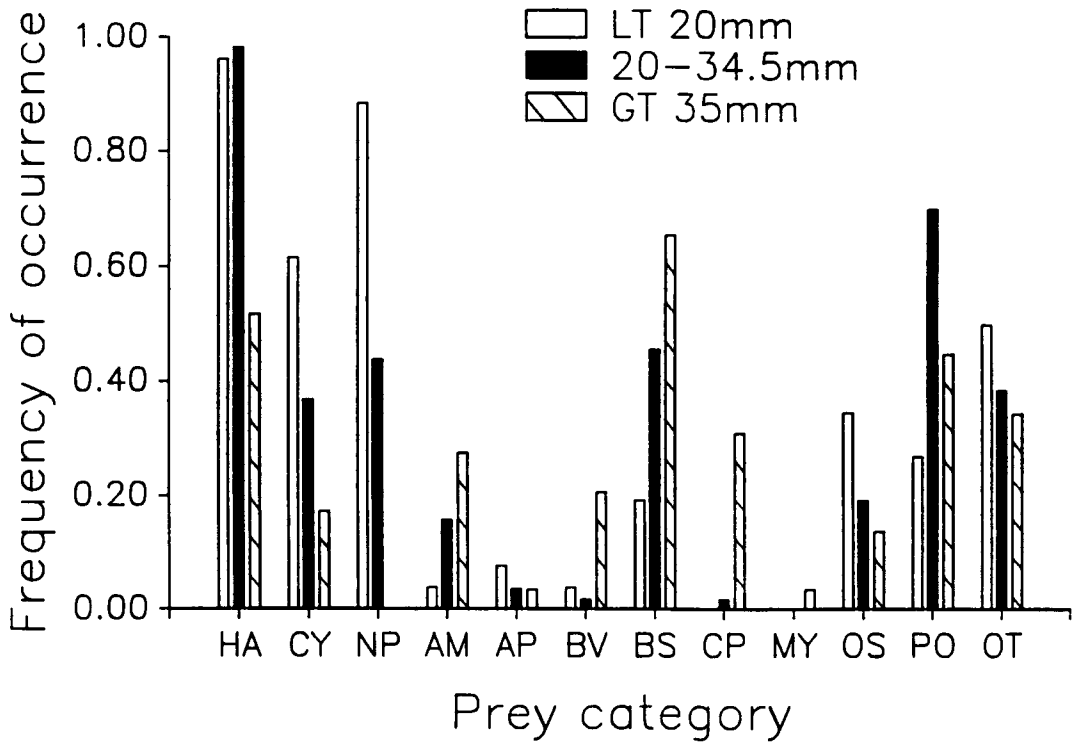

Figure 6. Frequencies of occurrence of prey categories from yellowfin sole of: A) less than 20.0 mm, B) 20.0 - 34.5 mm, and C) 35.0 mm and larger, standard length. Prey categories are abbreviated as in Table 2.

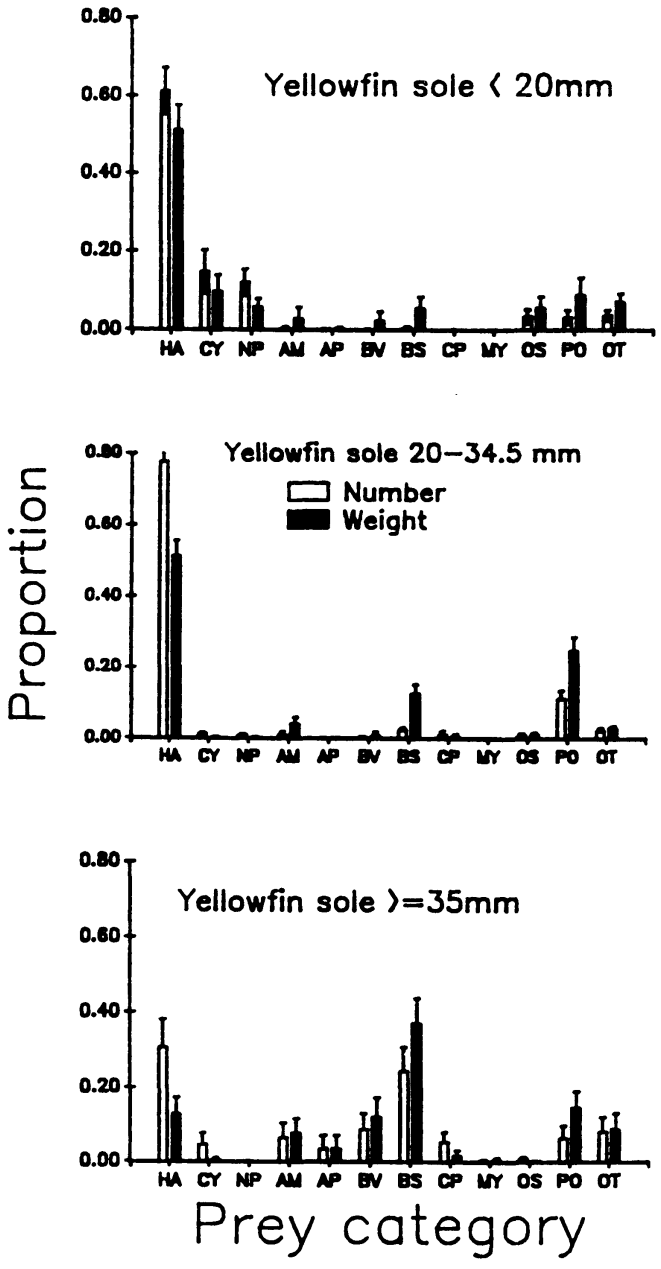

Figure 7. Proportion by number and weight of prey categories from yellowfin sole of: A) less than 20.0 mm, B) 20.0 - 34.5 mm, and C) 35.0 mm and larger, standard length. Prey categories are abbreviated as in Table 2. Vertical bars represent one standard error.

Within-Species Comparisons

Results of dietary comparisons of conspecifics of different size classes were similar using either numerical or weight data (Appendix E). Small and medium rock sole consumed a greater proportion of harpacticoids ($p<0.01$) and cyclopoids ($p<0.05$) than large rock sole. Medium rock sole consumed a greater proportion of amphipods than small fish ($p<0.01$). The diet of large rock sole was comprised of a higher proportion of bivalve siphons than in small or medium rock sole diets ($p<0.05$).

Small and medium starry flounder consumed greater proportions of harpacticoid and cyclopoid copepods than large fish ($p<0.01$). Small starry flounder consumed a greater proportion of copepod nauplii than large fish ($p<0.01$). The diets of medium and large starry flounder contained higher proportions of amphipods and mysids than small fish diets ($p<0.01$). Large starry flounder consumed a greater proportion of bivalve siphons ($p<0.01$) and polychaetes ($p<0.05$) than medium or small fish.

The diets of small and medium yellowfin sole contained greater proportions of harpacticoid copepods than the diet of large fish ($p<0.01$). In addition, small yellowfin sole consumed, numerically, a greater proportion of harpacticoids than medium fish and a greater proportion of cyclopoid copepods than medium or large fish ($p<0.05$). Medium

yellowfin consumed the greatest proportion of polychaetes ($p<0.05$). Large yellowfin consumed the greatest proportion of bivalve siphons ($p<0.01$), and small fish consumed the least proportion ($p<0.05$).

Within-Size Comparisons

Results of dietary comparisons of fish of different species, but within similar size classes, were similar with either numerical or weight data (Appendix F). Small fish of all three species fed primarily on harpacticoid and cyclopoid copepods. Small starry flounder consumed a larger proportion of harpacticoids than rock sole ($0<0.01$) or yellowfin sole ($p<0.05$), a smaller proportion of cyclopoids than rock sole ($p<0.01$) and numerically a smaller proportion than yellowfin sole ($p<0.05$). There was no significant difference in the proportion by weight of cyclopoids in the diets of starry flounder and yellowfin. Small yellowfin sole consumed a greater proportion of copepod nauplii than small rock sole or starry flounder ($p<0.01$).

The food of medium fish of all species was primarly harpacticoid copepods. No significant difference existed in the proportion of harpacticoids consumed by any species within this size class. Medium rock sole consumed a larger proportion of appendicularians ($p<0.05>$) and bivalves ($p<0.01$) than yellowfin sole. Starry flounder of this size

class consumed a greater proportion of mysids than yellowfin sole ($p<0.01$). Medium yellowfin consumed a greater proportion of polychaetes than rock sole ($p<0.05$) or starry flounder ($p<0.01$).

No significant differences were found in the dietary proportion of large rock sole and either other species, except that rock sole and yellowfin sole consumed greater proportions of barnacle cyprids than starry flounder ($p<0.01$). All other differences existed only between starry flounder and yellowfin sole. The primary food of all species of large fish was bivalve siphons. Starry flounder consumed greater proportions of bivalve siphons and mysids than yellowfin sole. Yellowfin consumed higher proportions of harpacticoid copepods and whole bivalves than starry flounder ($p<0.01$). Polychaetes were also consumed by all species; there was no significant difference in the proportional contribution to the diets by polychaetes.

Dietary Similarities

Positive correlations (Spearman Rank Order Correlation Coefficient; $p<0.05$) were found for eight pairs of fish diets when analysed by numerical proportion (Table 3). Diets of small fish of all species were correlated with each other, as were the diets of large rock sole with large starry flounder, small with medium rock sole, small with

Table 3. Spearman Rank Order Correlation Coefficients for numerical porportions of diet compositions for rock sole (RS), starry flounder (SF), and yellowfin sole (YS) of three size classes. Size classes are less than 20.0 mm (SM), 20 - 34.5 mm (MED), and 35.0 mm and larger (LG), standard length. An asterisk denotes a significant correlation.

	SMRS	MEDRS	LGRS	SMSF	MEDSF	LGSF	SMYS	MEDYS	LGYS
SMRS	1.00								
MEDRS	0.78*	1.00							
LGRS	-0.36	-0.13	1.00						
SMSF	0.79*	0.48	-0.32	1.00					
MEDSF	-0.01	0.16	0.26	0.06	1.00				
LGSF	-0.16	0.10	0.58*	-0.30	0.61*	1.00			
SMYS	0.77*	0.48	-0.37	0.77*	0.27	-0.16	1.00		
MEDYS	0.44	0.48	0.36	0.48	0.43	0.32	0.64*	1.00	
LGYS	0.09	0.47	0.34	-0.05	0.34	0.46	0.15	0.66*	1.00

medium yellowfin sole, medium with large starry flounder, and medium with large yellowfin.

Fish diets were clustered (cluster analysis of Spearman rank order correlation coefficient; Figure 8) into two main operational taxonomic units (OTU's) by numerical proportion. All small fish and medium rock sole were clustered in the first OTU. All other medium and all large fish were clustered in the second. The diets of small fish of all species were most similar (small rock sole - small starry flounder, 79% similarity; small yellowfin sole - other small fish, 77 % similarity). The two main OTU's were most dissimilar (7% similarity).

Positive correlations ($p<0.05$) were found for eight pairs of fish diets when analyzed by proportion by weight (Table 4). The diet of small yellowfin sole was correlated with those of small rock sole and small starry flounder. The diets of small and medium rock sole were also correlated. Also correlated were diets of medium and large starry flounder, diet of medium and large yellowfin sole, the diet of large starry flounder with those of large rock sole and large yellowfin sole, and the diets of medium rock sole and large yellowfin sole.

Fish diets were clustered (cluster analysis of Spearman rank order correlation coefficients; Figure 9) into two main OTU's when analyzed by proportion by weight. Again, all

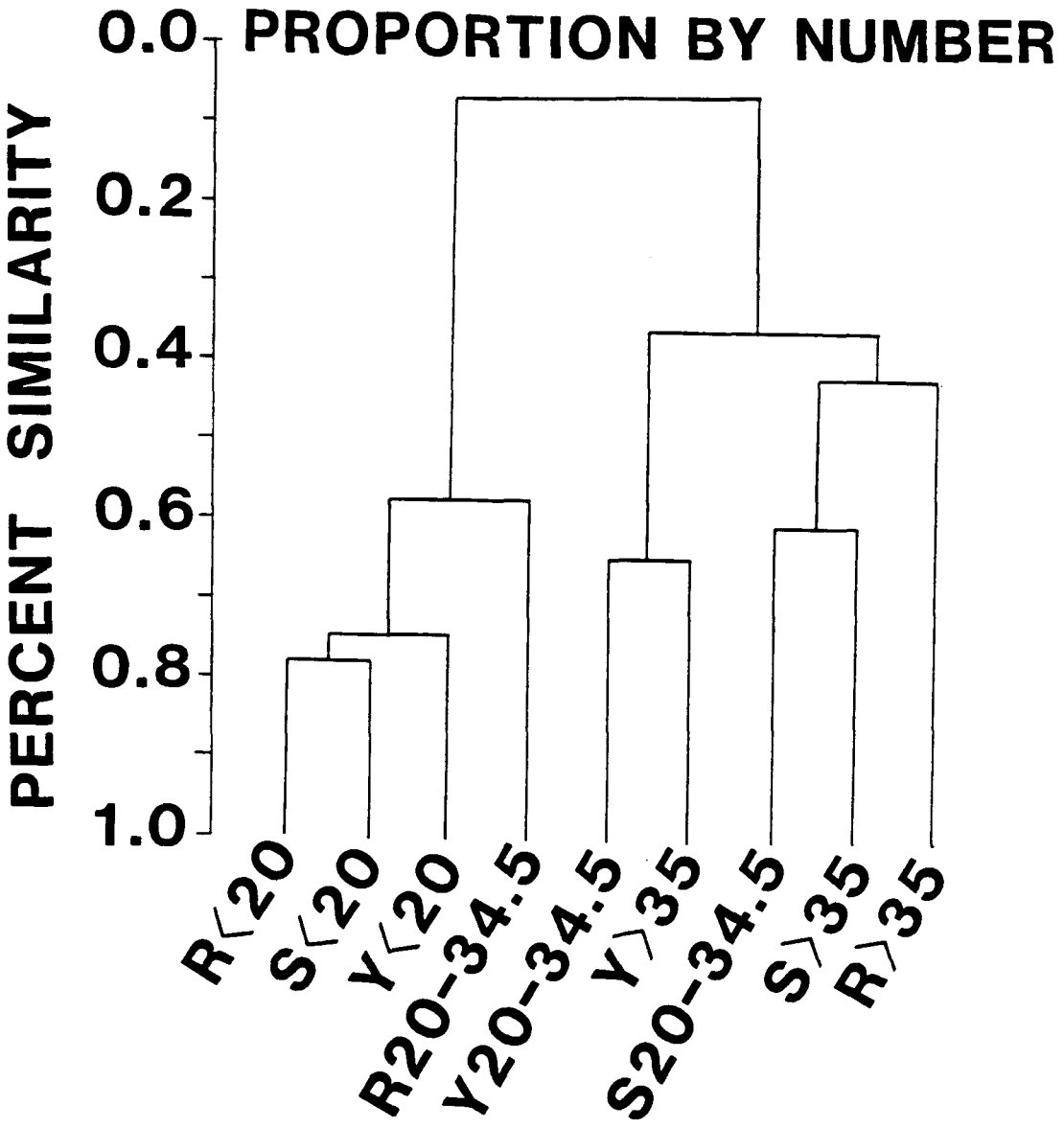

Figure 8. Clustering of similarity (Spearman Rank Order Correlation Coefficients) of numerical prey proportions found in the stomachs of rock sole (R), starry flounder (S), and yellowfin sole (Y) of three size classes. Size classes are less than 20.0mm (<20), 20.0-34.5mm (20-34.5) and 35mm and larger (>35).

Table 4. Spearman Rank Order Correlation Coefficients for proportion by weight of diet compositions for rock sole (RS), starry flounder (SF), and yellowfin sole (YS) of three size classes. Size classes are less than 20.0 mm (SM), 20.0-34.5 mm (MED), and 35.0 mm and larger (LG), standard length. An asterisk denotes a significant correlation.

	SMRS	MEDRS	LGRS	SMSF	MEDSF	LGSF	SMYS	MEDYS	LGYS
SMRS	1.00								
MEDRS	0.62*	1.00							
LGRS	-0.15	0.06	1.00						
SMSF	0.29	-0.11	-0.25	1.00					
MEDSF	0.09	0.40	0.27	0.16	1.00				
LGSF	0.03	0.19	0.72*	-0.15	0.68*	1.00			
SMYS	0.64*	0.20	-0.13	0.70*	0.37	0.13	1.00		
MEDYS	0.37	0.35	0.46	0.25	0.31	0.48	0.55	1.00	
LGYS	0.52	0.61*	0.54	-0.02	0.29	0.60*	0.24	0.73*	1.00

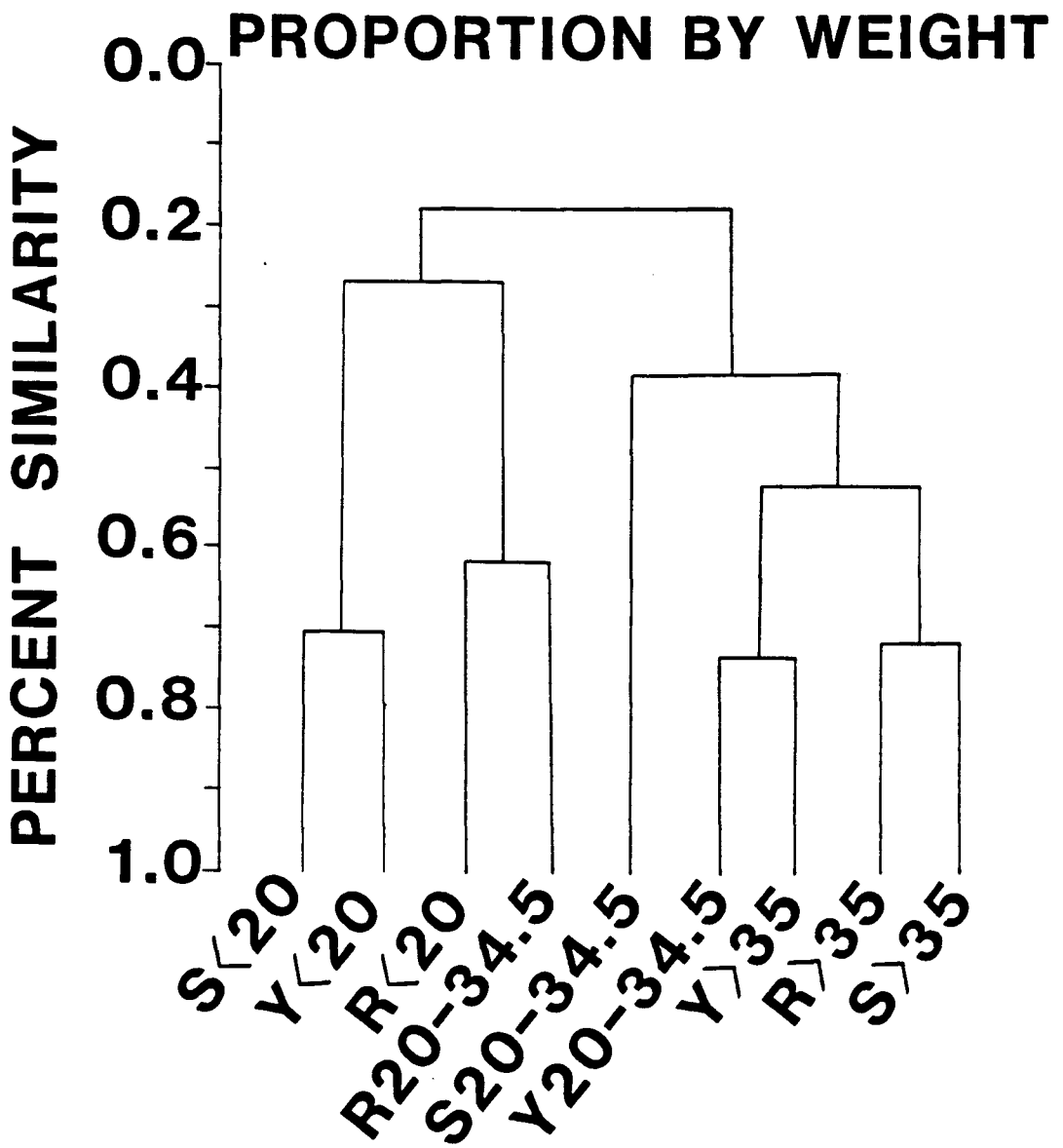

Figure 9. Clustering of similarity (Spearman Rank Order Correlation Coefficients) of prey proportions by weight found in the stomachs of rock sole (R), starry flounder (S), and yellowfin sole (Y) of three size classes. Size classes are less than 20.0mm (<20), 20.0-34.5mm (20-34.5) and 35mm and larger (>35).

small fish and medium rock sole were clustered into one OTU, and all other medium and all large fish were clustered into a second OTU. The diets of medium and large yellowfin sole, the diets of large rock sole and large starry flounder, and the diets of small starry flounder and small yellowfin were each paired at greater than 70% similarity. Least in similarity (18% similar) were the two main OTU's.

Timing of Settlement

Rock sole 23.0 mm SL were first collected on 10 July, 1987 (the first collection date of the year), starry flounder (9.5 mm) on 27 July, and yellowfin sole (13.5 mm) on 8 September. The following year rock sole young-of-the-year (13.5 mm) were first collected on 2 June, and starry flounder (9.0 mm) on 14 June. Sampling ended in July, 1988 and no newly metamorphosed yellowfin sole were collected.

Water temperatures varied from approximately 9°C to 15°C, and salinity varied from approximately 16 - 19°/oo, when newly settled rock sole and starry flounder were collected. Water temperatures varied from approximately 4°C-11°C, and salinity varied from approximately 19-30°/oo, when newly settled yellowfin sole were collected. Larger fish of all three species were collected throughout the year.

In both 1987 and 1988, the highest densities of

harpacticoid copepods occurred in mid-May (McGregor, chapter 1). Settlement of juvenile flatfish did not occur when harpacticoid densities were highest (Figure 10). In 1987 the numerical proportion of total meiofauna comprised of harpacticoids was highest on 16 June, and in 1988 on 2 June. In 1988 settlement of rock sole coincided exactly with the time when harpacticoids comprised their highest numerical proportion in the total meiofauna, and starry flounder followed shortly after (Figure 11). Settlement of yellowfin sole did not coincide in either year with periods of highest harpacticoid abundance.

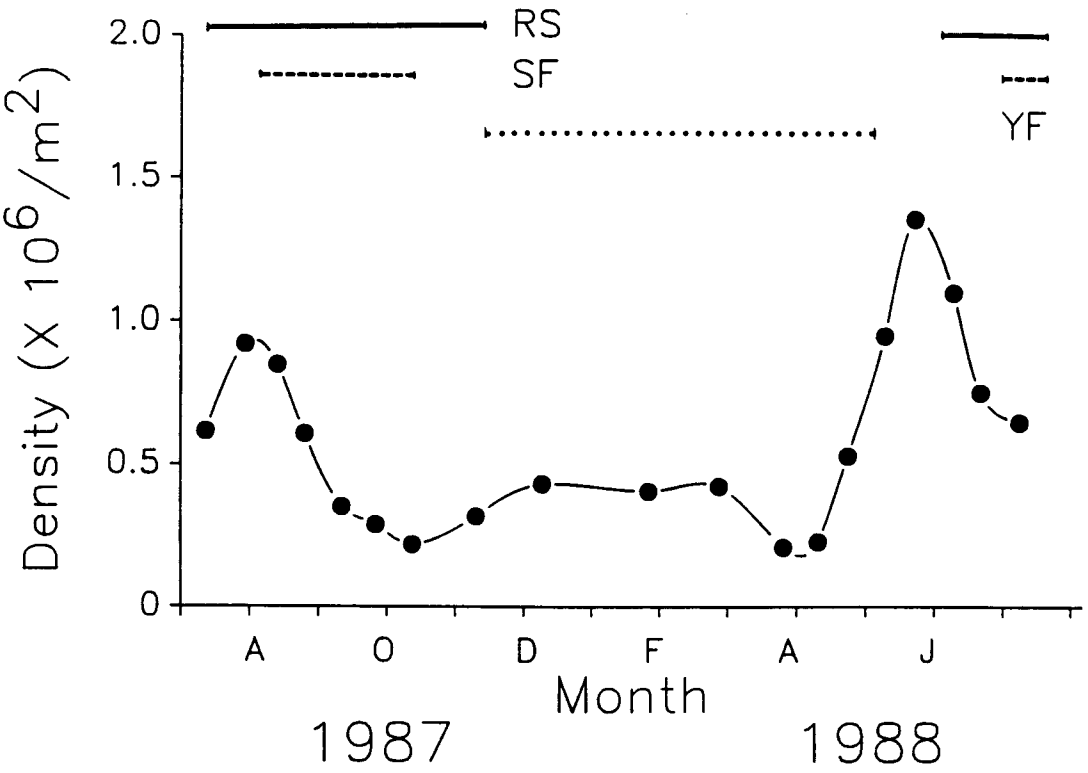

Figure 10. Time of collection of rock sole (RS), starry flounder (SF), and yellowfin sole (YS) less than 35.0 mm standard length, and harpacticoid copepod densities, 1987 - 1988.

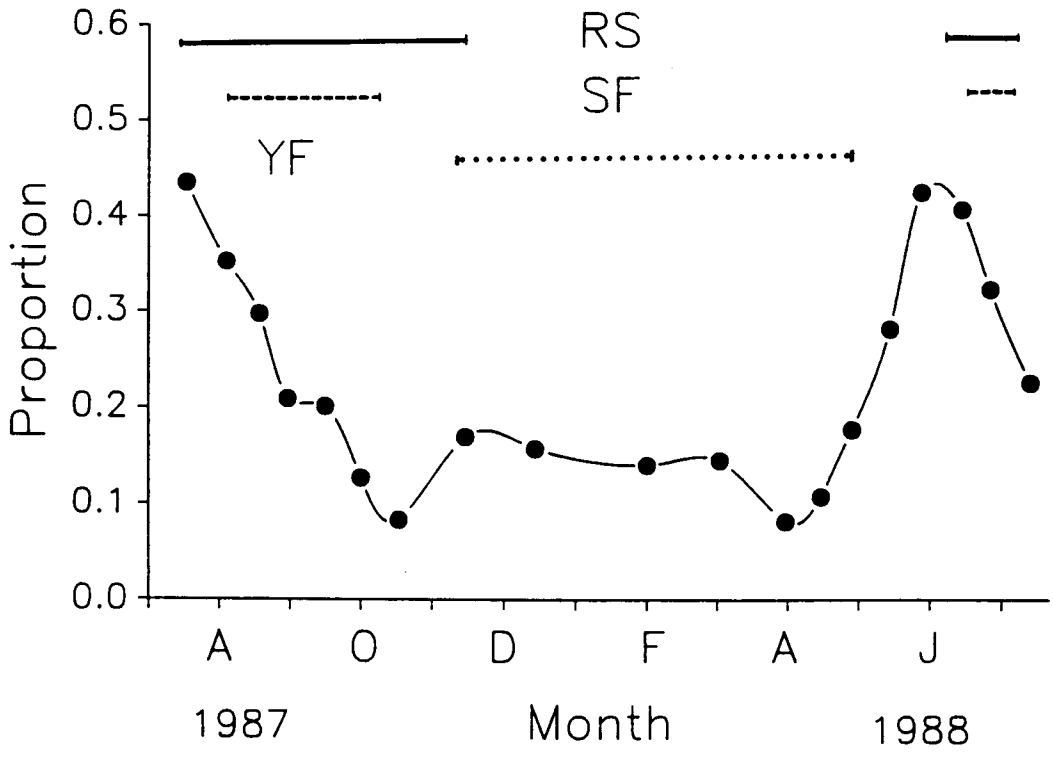

Figure 11. Time of collection of rock sole (RS), starry flounder (SF), and yellowfin sole (YS) less than 35 mm in length, and proportion of harpacticoid copepods in total meiofauna, 1987 - 1988.

DISCUSSION

Juvenile starry flounder have been the subjects of several dietary studies (Campana, 1984; Orcutt, 1950; Shirley et al., 1987; Sturdevant, 1987). The diets of juvenile rock sole and yellowfin sole, however, are less well known. Sturdevant (1987) reported that the diets of juvenile rock sole and yellowfin sole were dissimilar; however, the size range of the specimens examined did not overlap. I examined a fuller range of sizes (9.0 mm-97.0 mm SL) of all three species over the time interval of one year to attempt to follow ontogenetic changes in diets, as well as to compare the diets of similarly sized fish of different species.

In 1987, the smallest rock sole collected was 23.0 mm in length, while in 1988 the smallest rock sole was nearly 10 mm smaller (13.5 mm). It is possible that, sampling at two week intervals, I missed the earliest rock sole to settle in 1987. However, the timing of rock sole settlement was protracted in comparison to that of starry flounder and yellowfin sole, so I was able to sample most of the period of settlement during both years.

Rock sole and starry flounder settled at approximately the same time and a potential exists for the diets of the two species to overlap. However, starry flounder diets contained a significantly higher proportion of harpacticoid

copepods than rock sole diets, both numerically and by weight. Cyclopoid copepods comprised a significantly higher proportion in the diets of rock sole than starry flounder, both numerically and by weight. Rock sole consumed small proportions of prey types other than harpacticoids, while starry flounder diets were more restricted.

Differences in feeding behavior may decrease prey overlap between species. My analysis of the diets of similar sized rock sole and starry flounder supports this theory. Harpacticoids were comonly found in the surficial sediment of cores from the study site, and cyclopoids were uncommon (McGregor, chapter 1). Postmetamorphic rock sole have been observed to prey higher in the water column than similar sized starry flounder (Sturdevant, personal communication). Sturdevant suggested that such microhabitat use might be an important means of segregating rock sole and starry flounder.

Late settling rock sole may share resources with first settling yellowfin sole. Rock sole and yellowfin sole less than 35 mm SL were both present during the month of September. Diets of rock sole and yellowfin sole of this size were similar, both numerically and by weight, which may indicate competition for food resources. However, both species fed on a wider range of prey types than similar sized starry flounder.

There are several mechanisms rock sole and yellowfin sole could utilize to avoid competition. The two species may inhabit different microhabitats. Their similarity in diet would tend to refute this; however, the difference in diets may be at a prey-species level, which my study did not address. Other studies have shown that fish select certain species of harpacticoids over others (Alheit and Scheibel, 1982; Feller and Kaczynski, 1975; Hicks, 1984; Hicks, 1985; Morais and Bodiou, 1984). Partitioning of an important food resource at a species level should be examined as a possible means of sympatric species avoiding competition.

Harpacticoids may not be a limiting resource at the sample site during the time when flatfish are present. Harpacticoid densities recorded in May 1987 (prior to flatfish settlement) were among the highest ever recorded throughout the world (approximately 2.6 X $10^{6}/m^{2}$), and even "low" densities at the site were high compared to reports from other areas (see Hicks and Coull, 1983 for review; McGregor, chapter 1). During 1987 and 1988 similar trends in harpacticoid abundance were observed at the site, although absolute densities differed significantly. Highest annual densities were recorded in mid-May, followed by a dramatic decline in harpacticoid numbers throughout the summer of both years. Factors influencing changes in meiofaunal densities are not well understood. Predation has

been suggested by some authors as one possible means for reducing densities of harpacticoids (Feller and Kaczynski, 1975; Sibert, 1979). Other authors have refuted this idea, suggesting instead that only certain species of prey which are actively selected may be affected (Morais and Bodiou, 1984), that prey densities may only be temporarily affected when their densities decrease below maximum levels (Hicks, 1984; Hicks, 1985), or that the effect on prey populations is negligible (Alheit and Scheibel, 1982; Gee, 1987).

Predation may affect harpacticoid densities in spring at the study site. Salmon fry outmigrate from nearby creeks begining in March and continuing into May. Pink and chum salmon fry have been shown to feed primarily on harpacticoid copepods during their period of residency in the nearshore environment in Auke Bay (Landingham and Mothershed, 1988). The period of fry residency extends aproximately late March through early June (Mortensen and Wertheimer, 1988), overlapping the highest peak in harpacticoid abundances at the study site. Large numbers of salmon fry outmigrating in spring have been implicated in reductions in harpacticoid densities in Puget Sound (Feller and Kaczynski, 1975). In addition to salmon, many other juvenile fish and invertebrates were observed to utilize the study area in early spring (personal observation). While my study does not address predation by species other than flatfish, it is

possible that large numbers of salmon and other similar sized predators may contribute to reductions in harpacticoid populations in the spring.

Rock sole and starry flounder young-of-the-year were not collected until mid-June or early July in 1987 and 1988. By this time, salmon fry had largely moved offshore and were utilizing pelagic prey (Mortenson and Wertheimer, 1988). By June, harpacticoid densities were greatly reduced from maximum abundances in May, but were still relatively high (1987, 453,000/m^2; 1988, 681,290/m^2). Without predation pressure from large numbers of salmon fry, harpacticoid copepod densities may have been high enough to support spring-settling flatfish at the study site. However this may be a local phenomenon resulting from extremely high densities of harpacticoids at the site. In other areas where there are fewer harpacticoids, starry flounder and rock sole may have to partition resources; thus segregation of microhabitat might result.

Juvenile yellowfin sole habitat utilization and diet have previously been undescribed. The nearshore environment appears to be important to newly settled yellowfin, as well as to other species of postmetamorphic flatfish. Yellowfin sole settle at a time of the year when there are probably few other predators consuming meiofauna in the nearshore environment. Presumably most spring-settling fish and

invertebrates would have grown to a size where they would be utilizing larger prey, or have moved offshore, by September when yellowfin sole young-of-the-year were first collected. Despite the fact that harpacticoid densities were low when compared to spring densities at the site, their densities may be sufficient in the fall to support the few predators thought to be utilizing harpacticoids at that time.

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Appendix A. Grouping of sample dates for analysis of total meiofauna densities, proportion of gravid female harpacticoid copepods, densities of gravid female harpacticoids, densities of harpacticoid nauplii, densities of harpacticoid copepodites, densities of adult harpacticoids, the ratio of nauplii to adult harpacticoids, and densities of nematodes.

Group	Sample dates grouped for comparisons
Total meiofauna	3/22/89-6/16/87; 7/10/87-7/1/88
Proportion of gravid female harpacticoids	3/2/87 & 1/20/88-4/4/88; 4/5/87-12/4/87 & 4/17-88-7/1/88
Density of gravid female harpacticoids	3/2/87 & 1/20/88-3/20/88; 4/5/87-12/4/87 & 4/4/88-7/1/88
Density of harpacticoid nauplii	3/22/87-5/28/87; 6/16/87-11/5/87; 12/4/87-4/17/88; 5/3/88-7/1/88
Density of harpacticoid copepodites	3/22/87 & 7/10/87-4/4/88; 4/5/87-6/16/87 & 4/17/88-7/1/88
Density of adult harpacticoids	3/22/87-4/14/87; 5/1/87-6/16/87; 7/10/87-4/17/88; 5/3/88-7/1/88
Ratio of harpacticoid nauplii:adults	3/22/87 & 3/2/88; 4/5/87-2/20/88 & 4/4/88-7/1/88
Density of nematodes	3/22/87-3/28/87; 6/16/87-7/1/88

Appendix B. Density of meiofauna in #/cm**3 (SE) in Auke Bay for 1987 and 1988. Abbreviations are as in Chapter 2, Table 2, except for gravid harpacticoids (GH), harpacticoid copepodites (GH), copepods (CA), nematodes (NE), barnacle nauplii (BN), cumaceans (CU), halocarid mites (HAL), juvenile polychaetes (JPO), tardigrades (TA), turbellarians (TU), oligochaetes (OL), isopods (IS), total copepods (Tot Cope), total meiofauna (Tot Meio), and nauplii:harpacticoid ratio (Naup:Cope).

Julian Date	# cores	HA	GH	HC	NA	ES	CY
81	4	261.35	115.26	236.78	2301.66	12.96	0.45
		(48.69)	(22.13)	(47.06)	(223.18)	(3.13)	(0.45)
91	4	582.56	80.41	579.43	2864.11	10.28	0.00
		(36.15)	(17.97)	(66.31)	(638.38)	(4.28)	(0.00)
104	4	577.20	60.31	375.27	1774.49	12.06	0.45
		(27.28)	(8.67)	(36.04)	(178.57)	(2.57)	(0.45)
121	3	839.35	60.75	505.83	1777.37	16.67	0.68
		(90.86)	(3.38)	(103.17)	(467.39)	(2.87)	(0.52)
133	4	1769.13	69.69	804.15	1854.91	13.85	0.00
		(105.60)	(10.50)	(147.58)	(276.76)	(5.72)	(0.00)
148	4	1935.32	38.42	493.21	1227.67	10.28	0.00
		(73.85)	(6.79)	(121.62)	(208.30)	(3.75)	(0.00)
167	4	1665.48	20.55	323.45	503.93	2.68	0.00
		(199.14)	(3.89)	(76.06)	(88.44)	(1.15)	(0.00)
191	4	453.00	21.89	162.62	41.99	4.91	0.00
		(94.57)	(6.33)	(78.50)	(18.71)	(2.77)	(0.00)
208	4	781.37	35.74	138.49	84.44	4.02	0.00
		(73.26)	(9.68)	(58.30)	(14.65)	(2.35)	(0.00)
222	4	764.84	21.00	83.54	46.46	5.81	4.47
		(273.72)	(4.64)	(37.16)	(16.20)	(3.45)	(4.47)
234	4	499.91	43.78	108.11	58.97	8.94	1.34
		(127.03)	(10.83)	(68.69)	(25.74)	(2.19)	(0.86)
250	4	319.87	29.49	31.72	27.25	7.15	0.45
		(55.89)	(3.61)	(9.96)	(6.50)	(0.73)	(0.45)
265	4	264.03	43.78	24.57	47.80	12.96	0.45
		(27.02)	(8.89)	(5.94)	(15.50)	(3.89)	(0.45)
281	4	201.48	54.06	16.98	166.19	14.74	0.00
		(20.01)	(13.85)	(1.86)	(55.48)	(3.04)	(0.00)
309	4	276.09	36.63	42.44	115.26	3.57	0.00
		(81.25)	(14.23)	(7.20)	(46.77)	(1.63)	(0.00)
338	4	337.30	77.73	95.60	554.42	4.02	0.00
		(39.48)	(10.63)	(15.19)	(137.31)	(1.34)	(0.00)
20	4	357.85	158.60	49.14	681.74	12.51	0.00
		(62.21)	(27.90)	(14.67)	(157.95)	(4.25)	(0.00)

Appendix B. (cont.)

Julian Date	# cores	HA	GH	HC	NA	ES	CY
51	4	338.19	144.75	86.22	609.37	15.64	0.00
		(82.86)	(37.87)	(30.84)	(219.96)	(5.85)	(0.00)
79	3	253.41	126.03	64.71	768.88	10.54	0.00
		(41.09)	(22.39)	(4.64)	(153.47)	(1.29)	(0.00)
94	4	117.05	45.57	112.13	484.72	4.02	0.00
		(22.39)	(8.68)	(32.87)	(181.86)	(1.53)	(0.00)
107	4	250.18	61.20	280.11	808.17	4.47	0.45
		(11.72)	(9.88)	(43.87)	(168.70)	(2.13)	(0.45)
123	4	725.97	68.35	225.61	242.59	8.49	0.00
		(212.28)	(8.20)	(124.02)	(121.02)	(3.37)	(0.00)
136	4	1099.00	68.80	259.56	335.96	4.91	0.00
		(71.45)	(11.08)	(39.35)	(101.64)	(1.34)	(0.00)
153	4	1019.04	49.59	83.10	126.88	5.81	0.00
		(158.11)	(6.50)	(24.75)	(35.64)	(2.86)	(0.00)
165	4	681.29	19.66	72.37	196.12	5.81	0.00
		(128.52)	(2.31)	(10.12)	(22.90)	(1.53)	(0.00)
182	4	584.35	17.87	65.23	87.12	1.79	0.00
		(197.48)	(10.89)	(25.47)	(33.13)	(1.26)	(0.00)

Appendix B. (cont.)

Julian Date	CC	CA	CAC	NE	BN	CP
81	0.00	0.00	0.00	2333.82	0.00	0.00
	(0.00)	(0.00)	(0.00)	(257.49)	(0.00)	(0.00)
91	0.00	0.00	0.00	1919.24	0.00	0.00
	(0.00)	(0.00)	(0.00)	(283.08)	(0.00)	(0.00)
104	0.00	0.45	0.00	2852.05	8.04	0.00
	(0.00)	(0.45)	(0.00)	(389.78)	(5.90)	(0.00)
121	0.00	0.32	0.00	2392.38	5.34	0.00
	(0.00)	(0.00)	(0.00)	(268.89)	(0.52)	(0.00)
133	0.45	0.00	0.00	2482.14	0.00	0.00
	(0.45)	(0.00)	(0.00)	(787.99)	(0.00)	(0.00)
148	0.00	0.00	0.00	2480.36	0.00	0.00
	(0.00)	(0.00)	(0.00)	(717.91)	(0.00)	(0.00)
167	0.00	0.00	0.00	1704.80	0.00	4.47
	(0.00)	(0.00)	(0.00)	(274.83)	(0.00)	(2.36)
191	0.00	0.00	0.00	857.31	0.45	0.00
	(0.00)	(0.00)	(0.00)	(299.31)	(0.45)	(0.00)
208	0.45	0.45	0.00	1547.54	0.00	0.00
	(0.45)	(0.45)	(0.00)	(120.09)	(0.00)	(0.00)
222	1.34	0.00	0.00	1702.12	0.00	0.00
	(1.34)	(0.00)	(0.00)	(295.15)	(0.00)	(0.00)
234	0.00	0.00	0.00	1988.93	0.00	0.00
	(0.00)	(0.00)	(0.00)	(171.21)	(0.00)	(0.00)
250	0.00	0.00	0.45	1486.78	0.00	0.00
	(0.00)	(0.00)	(0.45)	(344.08)	(0.00)	(0.00)
265	0.00	0.00	0.00	2178.35	0.00	0.00
	(0.00)	(0.00)	(0.00)	(573.88)	(0.00)	(0.00)
281	0.00	0.00	0.00	2496.44	0.00	0.00
	(0.00)	(0.00)	(0.00)	(686.20)	(0.00)	(0.00)
309	0.00	0.45	0.00	1472.49	0.00	0.00
	(0.00)	(0.45)	(0.00)	(257.61)	(0.00)	(0.00)
338	0.00	0.00	0.00	1733.39	0.00	0.00
	(0.00)	(0.00)	(0.00)	(178.76)	(0.00)	(0.00)
20	0.00	0.45	0.00	1710.61	0.00	0.00
	(0.00)	(0.45)	(0.00)	(93.81)	(0.00)	(0.00)

Appendix B. (cont.)

Julian Date	CC	CA	CAC	NE	BN	CP
51	0.00	0.00	0.00	1695.86	0.00	0.00
	(0.00)	(0.00)	(0.00)	(190.70)	(0.00)	(0.00)
79	0.00	0.00	0.00	1553.46	0.36	0.00
	(0.00)	(0.00)	(0.00)	(84.64)	(0.49)	(0.00)
94	0.00	0.00	0.00	1424.24	0.89	0.00
	(0.00)	(0.00)	(0.00)	(220.01)	(0.52)	(0.00)
107	0.00	0.89	0.00	1658.34	0.45	0.00
	(0.00)	(0.89)	(0.00)	(133.95)	(0.45)	(0.00)
123	0.00	0.45	0.00	1935.32	0.45	0.00
	(0.00)	(0.45)	(0.00)	(224.65)	(0.45)	(0.00)
136	0.00	0.45	0.00	1495.72	0.89	1.34
	(0.00)	(0.45)	(0.00)	(199.70)	(0.89)	(0.86)
153	0.00	0.00	0.00	1431.39	0.00	1.34
	(0.00)	(0.00)	(0.00)	(217.99)	(0.00)	(0.86)
165	0.00	0.00	0.00	1324.17	0.00	1.34
	(0.00)	(0.00)	(0.00)	(221.86)	(0.00)	(0.86)
182	0.00	0.00	0.00	1887.07	0.00	0.89
	(0.00)	(0.00)	(0.00)	(389.04)	(0.00)	(0.52)

Appendix B. (cont.)

Julian Date	BV	CU	HAL	OS	PO	JPO
81	0.00	0.45	0.45	49.59	0.45	0.00
	(0.00)	(0.45)	(0.45)	(11.07)	(0.45)	(0.00)
91	0.00	0.00	0.89	65.23	0.00	0.00
	(0.00)	(0.00)	(0.89)	(10.93)	(0.00)	(0.00)
104	0.00	0.00	2.23	61.65	0.89	0.89
	(0.00)	(0.00)	(1.34)	(18.38)	(0.52)	(0.89)
121	0.00	0.36	2.35	77.57	1.58	0.64
	(0.00)	(0.52)	(0.00)	(15.89)	(0.89)	(0.00)
133	0.00	0.00	0.45	119.73	8.49	0.00
	(0.00)	(0.00)	(0.45)	(50.88)	(1.12)	(0.00)
148	0.00	0.00	2.23	56.29	6.70	0.45
	(0.00)	(0.00)	(0.45)	(12.81)	(0.86)	(0.45)
167	31.72	0.00	0.89	24.57	7.59	3.57
	(4.97)	(0.00)	(0.52)	(7.31)	(1.34)	(0.73)
191	1.79	0.45	1.34	25.46	0.45	0.00
	(1.26)	(0.45)	(0.45)	(13.75)	(0.45)	(0.00)
208	1.79	0.89	3.57	45.12	0.89	0.00
	(1.03)	(0.52)	(1.63)	(15.38)	(0.52)	(0.00)
222	0.00	0.00	1.34	64.78	0.89	0.00
	(0.00)	(0.00)	(0.86)	(26.02)	(0.52)	(0.00)
234	1.34	0.00	4.47	60.76	0.89	0.00
	(0.86)	(0.00)	(3.30)	(19.97)	(0.52)	(0.00)
250	0.00	0.00	3.13	35.74	0.00	0.00
	(0.00)	(0.00)	(0.86)	(13.27)	(0.00)	(0.00)
265	0.00	0.00	2.68	37.97	0.00	0.00
	(0.00)	(0.00)	(1.55)	(8.30)	(0.00)	(0.00)
281	0.45	0.00	2.23	45.12	0.00	0.00
	(0.45)	(0.00)	(0.86)	(7.84)	(0.00)	(0.00)
309	0.00	0.00	0.89	21.89	0.00	0.45
	(0.00)	(0.00)	(0.89)	(3.04)	(0.00)	(0.45)
338	0.00	0.00	5.36	41.99	0.00	0.00
	(0.00)	(0.00)	(1.93)	(8.46)	(0.00)	(0.00)
20	0.00	0.00	6.25	22.78	0.00	0.00
	(0.00)	(0.00)	(2.36)	(3.53)	(0.00)	(0.00)

Appendix B. (cont.)

Julian Date	BV	CU	HAL	OS	PO	JPO
51	0.00	0.00	4.02	23.23	0.00	0.00
	(0.00)	(0.00)	(1.69)	(2.83)	(0.00)	(0.00)
79	0.00	0.36	4.90	22.18	0.00	0.00
	(0.00)	(0.49)	(0.97)	(9.72)	(0.00)	(0.00)
94	0.00	0.00	2.23	11.62	0.00	0.00
	(0.00)	(0.00)	(1.69)	(3.30)	(0.00)	(0.00)
107	0.00	0.00	0.45	25.91	0.00	1.34
	(0.00)	(0.00)	(0.45)	(6.79)	(0.00)	(1.34)
123	0.00	0.00	1.79	16.08	0.00	0.00
	(0.00)	(0.00)	(0.73)	(4.25)	(0.00)	(0.00)
136	0.00	0.00	0.00	27.70	1.79	1.79
	(0.00)	(0.00)	(0.00)	(4.92)	(0.73)	(0.73)
153	3.13	0.00	4.02	24.57	3.13	3.57
	(1.34)	(0.00)	(1.98)	(1.69)	(1.53)	(2.42)
165	2.68	0.00	0.45	15.19	4.02	1.34
	(1.55)	(0.00)	(0.45)	(1.55)	(1.69)	(0.86)
182	0.89	0.00	0.45	16.53	0.00	1.79
	(0.89)	(0.00)	(0.45)	(8.61)	(0.00)	(1.26)

Appendix B. (cont.)

Julian Date	TA	TU	OL	IS	AM	Tot Cope
81	0.00	0.00	0.89	0.00	0.00	498.13
	(0.00)	(0.00)	(0.89)	(0.00)	(0.00)	(92.16)
91	0.00	0.00	0.45	0.45	0.00	1162.00
	(0.00)	(0.00)	(0.45)	(0.45)	(0.00)	(66.46)
104	0.00	0.00	1.34	0.00	0.00	952.47
	(0.00)	(0.00)	(0.86)	(0.00)	(0.00)	(55.78)
121	0.00	0.00	3.29	0.00	0.00	1345.18
	(0.00)	(0.00)	(3.61)	(0.00)	(0.00)	(191.23)
133	0.00	2.68	0.89	0.00	0.00	2573.28
	(0.00)	(2.13)	(0.89)	(0.00)	(0.00)	(250.83)
148	0.00	0.00	0.00	0.00	0.00	2428.53
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(161.38)
167	0.00	0.45	0.00	0.00	0.45	1988.93
	(0.00)	(0.45)	(0.00)	(0.00)	(0.45)	(273.75)
191	0.00	0.00	0.00	0.00	0.00	615.62
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(156.96)
208	0.45	0.00	0.00	0.00	0.00	919.86
	(0.45)	(0.00)	(0.00)	(0.00)	(0.00)	(89.82)
222	0.00	0.00	0.00	0.45	0.00	848.38
	(0.00)	(0.00)	(0.00)	(0.45)	(0.00)	(308.41)
234	0.00	0.00	0.00	0.00	0.00	608.03
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(194.30)
250	0.00	0.00	0.00	0.00	0.00	351.59
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(47.84)
265	0.00	0.00	0.00	0.00	0.00	288.60
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(31.13)
281	0.45	0.00	0.00	0.00	0.00	218.46
	(0.45)	(0.00)	(0.00)	(0.00)	(0.00)	(18.99)
309	0.00	0.00	0.00	0.00	0.00	318.53
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(75.75)
338	0.00	0.00	0.00	0.00	0.00	432.90
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(50.68)
20	0.00	0.00	0.00	0.00	0.00	406.99
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(66.29)

Appendix B. (cont.)

Julian Date	TA	TU	OL	IS	AM	Tot Cope
51	0.00	0.00	0.00	0.00	0.00	424.41
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(109.76)
79	0.00	0.00	0.00	0.00	0.00	318.13
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(43.10)
94	0.00	0.00	0.00	0.00	0.00	229.18
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(54.06)
107	0.00	0.45	0.00	0.00	0.00	530.29
	(0.00)	(0.45)	(0.00)	(0.00)	(0.00)	(33.59)
123	0.00	0.00	0.00	0.00	0.00	951.58
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(333.74)
136	0.45	0.45	0.00	0.00	0.00	1358.57
	(0.45)	(0.45)	(0.00)	(0.00)	(0.00)	(32.22)
153	0.00	0.00	0.00	0.00	0.00	1102.13
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(182.68)
165	0.00	0.89	0.00	0.00	0.45	753.67
	(0.00)	(0.52)	(0.00)	(0.00)	(0.45)	(135.55)
182	0.00	0.00	0.00	0.00	0.00	649.57
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(216.11)

Appendix B. (cont.)

Julian Date	Tot Meio	Naup:cope
81	5185.87	9.10
	(255.80)	(1.71)
91	6012.36	4.29
	(958.15)	(0.84)
104	5654.96	3.41
	(366.48)	(0.52)
121	3750.91	1.88
	(835.81)	(0.26)
133	7043.01	1.27
	(698.97)	(0.07)
148	6202.23	0.89
	(690.84)	(0.11)
167	4271.38	0.48
	(203.06)	(0.10)
191	1544.86	0.13
	(458.00)	(0.04)
208	2605.45	0.17
	(214.67)	(0.03)
222	2670.22	0.14
	(450.87)	(0.07)
234	2724.73	0.21
	(398.47)	(0.11)
250	1905.39	0.14
	(364.44)	(0.03)
265	2555.86	0.28
	(623.22)	(0.06)
281	2929.34	1.43
	(651.63)	(0.52)
309	1929.96	0.69
	(313.63)	(0.32)
338	2768.06	2.26
	(275.62)	(0.46)
20	2828.82	3.00
	(273.18)	(0.42)

Appendix B. (cont.)

Julian Date	Tot Meio	Naup:cope
51	2756.89	2.26
	(278.96)	(0.55)
79	1525.50	6.75
	(190.81)	(0.08)
94	2152.89	3.52
	(308.84)	(0.61)
107	3026.73	2.68
	(264.88)	(0.49)
123	3148.25	0.38
	(637.04)	(0.09)
136	3225.09	0.45
	(202.88)	(0.15)
153	2700.16	0.20
	(129.44)	(0.03)
165	2300.32	0.53
	(330.71)	(0.13)
182	2644.31	0.37
	(613.54)	(0.18)

Appendix C. Water temperature, salinity, and collection dates for fish and meiofauna samples. An asterisk indicates no data available. A double asterisk indicates data obtained from Dr. Bruce Wing, N.M.F.S., Juneau, Alaska.

Date	H20 Temp (°C)	Salinity (°/oo)	Sampled
7/10/87	13.6 **	*	fish; meiof
7/14/87	13.8 **	*	fish
7/27/87	11.8 **	*	fish; meiof
8/10/87	15.0	16	meiof
8/11/87	13.7 **	*	fish
8/23/87	11.5	17	fish; meiof
9/8/87	11.0	19	fish; meiof
9/23/87	9.0	16	fish; meiof
10/8/87	7.3	24	fish; meiof
11/5/87	6.4	24	fish; meiof
12/4/87	5.1	*	fish; meiof
1/20/88	4.5	31	fish; meiof
2/20/88	4.3	24	fish; meiof
3/20/88	3.6	30	fish; meiof
4/4/87	*	*	fish; meiof
4/17/88	4.9	31	fish; meiof
5/3/88	7.5	29	fish; meiof
5/16/88	8.4	27	fish; meiof
6/2/88	10.5	23	fish; meiof
6/14/88	12.0	16	fish; meiof
7/1/88	11.9	18	fish; meiof

Appendix D. Summary of species and sizes of fish and dates of collection for 1987 and 1988. All measurements are standard length.

Rock sole		Starry flcunder		Yellowfin sole	
Date	Length	Date	Length	Date	Length
7/10	24.5	7/10	60.5	7/10	40.5
	24.0	7/14	73.0		47.5
	23.0		73.0	7/14	36.0
7/14	36.0		80.0		51.5
	28.5		71.0		50.0
7/27	12.5		70.5		52.0
8/11	30.0		76.0		47.5
8/23	13		80.0		37.0
	21.0		101.0		46.5
	13.5		77.5		37.5
	13.0		85.0		48.5
	13.0		86.5		34.5
	13.5	7/27	86.0	7/27	43.0
9/8	18.0		15.0	8/11	no fish
	18.0		20.0	8/23	no fish
	17.5		14.5	9/8	79.0
	15.5		16.0		78.0
	14.0		16.0		66.0
	14.5		14.0		65.0
	14.0		14.0		20.0
	15.0		13.0		16.0
	15.5		12.0		14.0
	44.4		13.5		13.0
	14.0		12.5		13.5
	23.5		13.0	9/23	no fish
	23.0		13.0	10/8	64.0
	24.0		12.0		68.0
	14.5		12.5		71.0
	14.5		9.5		60.0
	14.5	8/11	80.0		23.5
	12.5		22.0		22.0
9/23	no fish		13.5		17.0
10/8	49.5		97.0		18.0
	33.0		24.0		16.5
	30.5		18.5		14.0
	26.0		21.5		16.5
	27.0		18.0		18.0
	22.5		16.5		18.0
	24.5		11.0		15.0
	24.0		13.5		16.0
	21.5		12.5		13.0
	22.0		9.5		13.5
	22.0	8/23	36.5		12.5
	19.5		34.5		11.5

	16.0		28.0	11/5	23.5
11/5	no fish		28.0		27.0
12/4	64.5		27.0		25.0
1/20	no fish		26.0		22.0
2/20	no fish		24.5		25.0
3/20	no fish		25.5		26.0
4/4	no fish	9/8	no fish		26.0
4/17	80.0	9/23	34.0		26.5
5/3	no fish		28.0		25.0
5/16	no fish		23.5		24.0
6/2	14.0		24.0		23.5
	13.5	10/8	no fish		24.0
	13.5	11/5	no fish		23.0
6/14	21.5	12/4	34.5		21.0
	16.0	1/20	34.5		21.5
	16.5	2/20	47.0		22.5
	17.5		37.0		21.5
	14.0		36.0		21.0
	24.0	3/20	59.0		19.0
7/1	no fish		60.5		19.5
			53.5		18.0
			52.0		17.0
			49.0		19.0
		4/4	59.0	12/4	28.5
			58.0		28.5
			58.5		28.0
			56.5		26.0
			54.0		22.0
			48.5		21.5
			40.5		23.0
			40.5		20.0
			39.0		19.0
		4/17	76.5		21.0
			79.0		16.0
			72.0	1/20	40.0
			66.0		34.5
			55.0		29.5
			55.0		28.5
			40.0		26.0
		5/3	70.0		25.5
			73.0		28.0
			73.0		28.0
			71.0		29.0
			70.0		26.0
			63.0		24.5
			55.0		24.5
			52.0		24.0
		5/16	81.0		25.0
			74.0		24.5

Appendix D. (cont.)

	73.0		25.0
	70.0		23.0
	70.0		23.0
6/2	90.0		21.5
	66.0		22.0
6/14	9.5		20.5
	10.0		21.5
	9.0		20.0
	9.5		20.0
	69.0		19.5
7/1	85.0		19.5
	16.0		19.0
	13.0		19.0
	15.0	2/20	no fish
	12.0	3/20	no fish
	13.5	4/4	no fish
	14.0	4/17	35.0
	13.5		35.0
	12.0		34.5
	12.5		33.0
	11.5	5/3	73.0
	12.0		51.0
	11.0		45.0
	11.0		43.0
	12.0		42.0
	10.0		37.5
	9.0		36.5
	10.0		33.5
	9.0		30.0
	9.0	5/16	no fish
	9.0	6/2	49.0
			44.0
			44.0
			42.0
			39.0
			35.0
			35.5
		6/14	33.5
			49.0
		7/1	no fish

Appendix E. Comparisons of proportion by number and by weight of the diets of three sizes of rock sole, starry flounder, and yellowfin sole (Mann Whitney U test). Size categories are less than 20.0mm (SM), 20.0-34.5mm (MED), and 35.0mm and larger (LG), standard length. Prey categories are as in Table 1.

Proportion by number, rock sole

	SM vs. MED	SM vs. LG.	MED vs. LG.
HA	0.549	0.003	0.003
CY	0.123	0.018	0.052
AM	0.005	0.185	0.735
BS	0.423	0.006	0.034
PO	0.035	0.018	0.295

Proportion by weight, rock sole

HA	0.670	0.003	0.005
CY	0.083	0.018	0.052
AM	0.004	0.185	0.553
BS	0.489	0.011	0.051
PO	0.048	0.018	0.245

Proportion by number, starry flounder

	SM vs. MED	SM vs. LG	MED vs. LG
HA	0.074	1.8 E-15	2.1 E-6
CY	0.597	6.0 E-5	3.1 E-5
NA	0.068	2.9 E-4	0.317
AM	0.001	0.007	0.316
BS	0.068	4.0 E-11	1.7 E-4
MY	0.001	2.6 E-6	0.570
PO	0.885	0.002	0.051

Proportion by weight, starry flounder

HA	0.046	1.8 E-15	4.2 E-6
CY	0.576	6.0 E-5	3.1 E-5
NA	0.068	2.9 E-4	0.317
AM	0.001	0.007	0.316
BS	0.068	4.0 E-11	1.7 E-4
MY	0.001	2.6 E-6	0.570
PO	0.885	7.4 E-4	0.029

Proportion by number, yellowfin sole

	SM vs. MED	SM vs. LG.	MED vs. LG
HA	0.010	0.005	3.1 E-6
CY	0.046	0.018	0.240
NA	1.3 E-4	2.1 E-7	4.9 E-5
BV	0.592	0.049	0.002
BS	0.015	4.9 E-5	0.001
CP	0.516	0.002	6.7 E-5
PO	2.9 E-4	0.134	0.017

Appendix E. (continued)

	Proportion by weight, yellowfin sole		
HA	0.976	6.6 E-6	7.7 E-8
CY	0.035	0.004	0.042
NA	1.0 E-6	2.1 E-7	4.9 E-5
BV	0.567	0.060	0.002
BS	0.028	1.3 E-4	0.002
CP	0.516	0.002	7.2 E-5
PO	4.8 E-4	0.134	0.065

Appendix F. Comparisons of proportion by number and by weight of the diets of rock sole (RS), starry flounder (SF), and yellowfin sole (YS) of small (less than 20.0mm), medium (20.0-34.5mm) and large (35.0mm and larger) size (standard length) classes (Mann Whitney U test). Prey categories are abbreviated as in Table 1. NS denotes comparison was not significantly different with Kruskal Wallis test, so was not tested with Mann Whitney U test.

	RS vs. SF	RS vs. YS	SF vs. YS
Proportion by number, small fish			
HA	0.009	0.481	0.019
CY	3.9 E-5	0.070	0.020
NP	0.550	3.8 E-4	3.1 E-5
BS	0.027	0.560	0.006
OS	0.052	0.152	3.9 E-4
OT	2.3 E-5	0.005	0.039
Proportion by weight, small fish			
HA	6.3 E-5	0.534	4.3 E-5
CY	3.1 E-4	0.059	0.067
NP	0.416	2.6 E-4	1.9 E-4
BS	0.027	0.540	0.004
OS	0.046	0.126	0.003
OT	NS	NS	NS
Proportion by number, medium fish			
	RS vs. SF	RS vs. YS	SF vs. YS
NP	0.167	0.049	6.0 E-4
AP	0.102	0.013	0.531
BV	0.062	7.8 E-4	0.674
BS	0.375	0.129	0.027
MY	0.102	0.089	1.4 E-4
PO	0.085	0.025	0.002
OT	NS	NS	NS
Proportion by weight, medium fish			
NP	0.167	0.059	0.006
AP	0.102	0.012	0.531
BV	0.062	7.8 E-4	0.674
BS	0.311	0.065	0.012
MY	0.102	0.089	1.4 E-4
PO	0.055	0.005	3.5 E-4
OT	0.839	0.026	0.098

Appendix F. (continued)

	RS vs. SF	RS vs. YS	SF vs. YS
	Proportion by number, large fish		
HA	0.954	0.152	0.001
CY	0.317	0.334	0.002
BV	0.800	0.279	0.004
BS	0.600	0.539	0.008
CP	0.002	0.829	2.5 E-5
MY	0.346	0.163	2.9 E-4
OS	0.317	0.400	0.007
OT	NS	NS	NS
	Proportion by weight, large fish		
HA	0.688	0.111	0.006
CY	0.317	0.334	0.002
BV	0.800	0.279	0.004
BS	0.621	0.838	0.127
CP	0.002	0.829	2.5 E-5
MY	0.313	0.163	3.2 E-4
OS	0.317	0.400	0.007
OT	0.286	0.025	1.4 E-4